FACTORS INFLUENCING THE UTILIZATION OF WOODY PLANTS AND FORBS BY UNGULATES

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ABSTRACT

The objective of this study was to determine the chemical, physical and phenological factors influencing the patterns of utilization experienced by different species of woody plants and forbs by browsing ungulates.

Field work was carried out in the Nylsvley Nature Reserve. Observations were made on hand-reared kudus, impalas and goats ranging freely in a 213 hectare enclosure. The feeding behaviour of a focal animal was recorded verbally on a tape-recorder, while the plants available were recorded along the path of movement of this animal. Plant samples were analysed quantitatively for nutrients, fibre constituents and polyphenols, and for the presence or absence of potential toxins, using standard techniques. The acceptance of plant species was assessed by the ratio number of plants eaten / number encountered. Statistical procedures entailed least squares correlations for single factors, Principal Components and Discriminant Function analyses.

The following correlations between acceptance and chemical factors were found:-

1. For woody plants there was no significant correlation with leaf nitrogen, except for kudus for the early growing season.
2. The only correlations with mineral nutrients were for phosphorus for kudus in the early growing season and for magnesium for all the animals in the dry season.

3. One nutrient rich species dominated the correlations for forbs, otherwise there were no significant correlations with nutrients.
4. There were no significant correlations with fibre components, except for a negative relationship with NDF and ADF for kudus in the late dry season.
5. There were no correlations with total polyphenols apart from a weak positive correlation for impalas.
6. Overall correlations with condensed tannins were not significant, but all plants containing more than 5% concentration showed low acceptances.
7. No influence by plant toxins was detected.

Acceptances were not correlated to bite sizes or rates of food intake achieved.

Discriminant Function analysis distinguished between preferred and non-preferred woody plants on the basis of nitrogen plus condensed tannin contents. The first Principal Components axis was based on concentrations of nutrients versus fibre and condensed tannins.

Findings suggest that high contents of condensed tannins, but not other polyphenols, are a feeding deterrent, with nutrient and fibre concentrations being of secondary importance. Structural deterrents modify food preference by limiting intake rates. The functional effect of condensed tannins is postulated to be to restrict microbial fermentation of cell wall tissues. Thus, through the effect on the symbiotic microflora in the rumen, plant species rich in condensed tannins may be of low digestibility to ruminant browsers.

DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

.........S. M. Cooper.........

...12th.......Day of.....March.......,19.85..

PREFACE

Previous studies on the utilization of vegetation by large ungulates have commonly focussed on the selection of plant species without considering the underlying factors governing this selection. Where plant chemistry has been considered, the scope has been restricted to contents of crude protein and some of the mineral nutrients. No previous study in Southern Africa has covered the complete range of nutrient, fibre and secondary chemical concentrations in plant tissues that could influence patterns of food selection, nor have the effects of physical structures such as thorns been considered quantitatively.

This study was carried out under the auspices of the South African Savanna Ecosystem Project. From an ecosystem perspective the need was to understand the factors controlling the consumption of particular vegetation components by large herbivores. The study was undertaken with a companion project by R.N. Owen-Smith investigating the diet selection strategies of ungulates in response to vegetation conditions.

The purpose of this study was thus to record the patterns of selection of particular vegetation components by representative species of ungulate, and to relate measures of food preference for particular species to the chemical and physical properties of these species.

Funding was received from the Cooperative Scientific Programmes Division (now incorporated into the Foundation for Research Development), of the Council for Scientific and Industrial Research. Nutrient and fibre analyses were contracted out to the National Food Research Institute, C.S.I.R. Total polyphenols were analysed at the Sorghum Beer Unit. I thank Prof. J.L.C. Marais amd Dr. C.W. Glennie for help and advice on the analysis of secondary chemicals, and Miss D. Fiel for technical assistance. For advice and discussion I thank my supervisor Dr. R.N. Owen-Smith, and Dr J.B. Bryant and many of my collegues in the Centre for Resource Ecology. Thanks are also extended to the staff of the Savanna Ecosystem Project at Nylsvley.

LIST OF ABBREVIATIONS

Through out the thesis the following abbreviations are used on the figures to denote plant species names:-

1. Woody Plants

AN = *Acacia nilotica*
AT = *Acacia tortilis*
BA = *Burkea africana*
CM = *Combretum molle*
DC = *Dichrostachys cinerea*
DR = *Dombeya rotundifolia*
EN = *Euclea natalensis*
GF = *Grewia flavescens*
OP = *Ochna pulchra*
PA = *Peltophorum africanum*
RL = *Rhus leptodictya*
SP = *Strychnos pungens*
TS = *Terminalia sericea*
VR = *Vitex rehmannii*

2. Forbs

EA = *Evolvulus alsinoides*
HG = *Hermannia grisea*
IM = *Indigofera macra*
JF = *Justicia flava*
OH = *Oldenlandia herbacea*
PO = *Pollichia campestris*
SI = *Sida cordifolia*
SO = *Solanum panduraeforme*
TF = *Tephrosia forbesii*
WI = *Waltheria indica*

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CHAPTER 1.

INTRODUCTION

Large herbivores appear to be surrounded by a superabundance of food, yet only a small fraction of the dicotyledonous browse is eaten, and even then the use of browse species varies seasonally. This study was initiated in order to discover what chemical and structural attributes of a plant determine whether or not it is eaten by browsing ungulates.

Browse plants contain not only nutrients and fibre, but also a diverse array of secondary compounds. These compounds were so named because no primary metabolic function could be attributed to them (Sachs 1875, Fraenkel 1959). Numerous physiological functions have been suggested for these compounds (Seigler & Price 1976, Chew & Rodman 1979), but many plant secondary compounds appear to have an ecological role in defending the plant against attack by pathogens and herbivores (Rosenthal & Janzen 1974).

It has been suggested that the chemical defences of plants evolved primarily against microbial pathogens and insects, the vertebrate herbivores being innocent victims of this evolutionary "arms war" (Janzen 1978). However in ecosystems such as savannas, where the browsing pressure from vertebrates is historically high, plants are likely to have evolved defences directed at vertebrate herbivores (Brown 1960, Janzen 1978).

Whether or not plant defences are directly aimed at large herbivores the animals must still evolve methods of circumventing these defences, either through avoidance or detoxification, if they are to survive.

Many studies describe the species selection of browsing mammals in specific habitats but without investigating the underlying reasons for the selectivity of feeding observed. The work that has been done on plant chemistry in relation to species selection by browsers has mainly considered non-ruminant animals such as hares (Bryant 1981, Sinclair & Smith 1984) and primates (Milton 1975, Oates et. al. 1980, Glander 1981). The only studies on ruminant browsers consider deer in north America (Radwan & Crouch 1974, Vangilder et. al. 1982) and caribou in Alaska (Kuropat & Bryant 1980).

The number and diversity of ruminant browsers is greater in Africa than on any other continent but, as yet, there has been no detailed investigation of the chemical and structural attributes of the plants which may be responsible for determining the consumption of browse plants by both wild and domesticated browsing ungulates in Africa (Bell 1982).

In this study it is hoped to determine the nutritive and defensive characteristics of selected savanna plants and relate these to the degree and pattern of utilisation of these plants by common species of browsing ungulates.

As a basis for the study three major hypotheses were developed from the current practical and theoretical literature on the subject.

The hypotheses underlying this study are:-

1. Browse plants employ chemical and / or structural deterrents against herbivory. The chemical defences fall into two categories, digestion-reducing substances such as tannins, which are found mainly in the mature foliage of woody plants, while forbs and new leaves tend to be defended by toxins such as alkaloids. Plants utilising structural deterrents, often thorns or spines, possess less chemical defences (Feeny 1976, Rhoades & Cates 1976).

2. Herbivores select plant species to maximise their nutrient intake and minimise the intake of defensive chemicals. Large herbivores exert careful selection not only for plant species but for plant parts of specific phenological states. This selection may be relaxed under conditons of low food availability (Westoby 1974, Kuropat & Bryant 1980).

3. Pure browsers may be more able to cope with plant defence chemicals than mixed feeders which preferentially eat grass. Alien ungulates might be more sensitive to the effects of defences of indigenous browse plants and less able to detect their presence than animals which have evolved with the

vegetation (Arnold & Hill 1972, Laycock 1978).

In order to test these hypotheses the following key questions were asked:-

1. What is the relative importance of the following sets of factors in controlling the degree and timing of consumption of different species of woody plants and forbs?
   i. Nutrient concentrations
   ii. Structural deterrents
   iii. Chemical deterrents.

2. How do different species of browsing ungulates vary in their response to these features?

Three common species of ungulates were chosen to represent examples from a pure browser to a preferential grazer capable of extensive utilisation of browse. The animals also represent indigenous and alien, domesticated browsers. The animal species chosen were:-

1. The greater kudu (Tragelaphus strepsiceros strepsiceros Pallas). This is a large browsing ungulate of 180 - 300 Kg in weight, widely distributed throughout Africa from the Cape in the South to Somalia in the North (Dorst & Dandelot 1970). Kudus are specialist browsers and occur in a variety of habitats from woodlands to shrub savannas in both moist and arid regions (Pienaar 1974).

2. The impalas (Aepyceros melampus melampus Lichenstein) is a medium sized antelope of 40 - 55 Kg. This is a mixed grazer-browser showing a preference for green grass (Monro 1979). Impalas occur over large areas of eastern and southern Africa in fairly open wooded savannas, and show a preference for ecotones, short grass areas and disturbed sites (Dasman & Mossman 1962, Jarman & Jarman 1974, Hirst 1975, Leuthold 1970).

3. The boer goat (Capra hircus) is a common meat producing breed in Southern Africa, and is better adapted to the climate of the bushveld than are the mohair producing angora goats farmed in the more arid regions (Donaldson 1979). Goats are mixed feeders capable of utilising both grass and browse. The young females used in this study were of the "improved" boer goat breed and weighed between 30 and 35 Kg each.

There are two major types of savannas in Southern Africa. The broad leaf tall tree savannas and woodlands and the microphyllous short tree savannas. These two forms mix in a mosaic due to edaphic factors such as soil nutrient status (Huntly 1978).

This study was undertaken at the South African Savanna Ecosystem Project Study Site in the Nylsvley Nature Reserve where the mosaic was fine enough for both types of savannas to be encompassed within the small area of the enclosure in which the tame animals were kept.

CHAPTER 2.

DESCRIPTION OF THE STUDY AREA

2.1. Location of the Study Site

This study was conducted at the South African Savanna Ecosystem Project study site within the Nylsvley Nature Reserve in the northern Transvaal.(Latitude 24'29'S, longtitude 28'42'E). The reserve is 3120 ha in extent and lies 10 km south of Naboomspruit.

The SASEP study area covers an area of 745 ha to the south of the Nyl River floodplain (Huntley 1978). The southeastern corner of which was game-fenced to form a 213 ha enclosure in which the animals used in this study were kept. (*Fig.* 2.1.)

2.2. An Introduction to Savannas

Savannas occur between the equatorial rainforests and the semi-deserts of Africa, Australia and South America. The term savanna encompasses a range of vegetation types from closed woodlands with an understorey of grass, through open savanna woodlands as are found at Nylsvley, to treeless edaphic grasslands. In all cases the herbaceous layer is dominated by the C4 grasses.

Savannas cover 65% of the African continent. Southern african

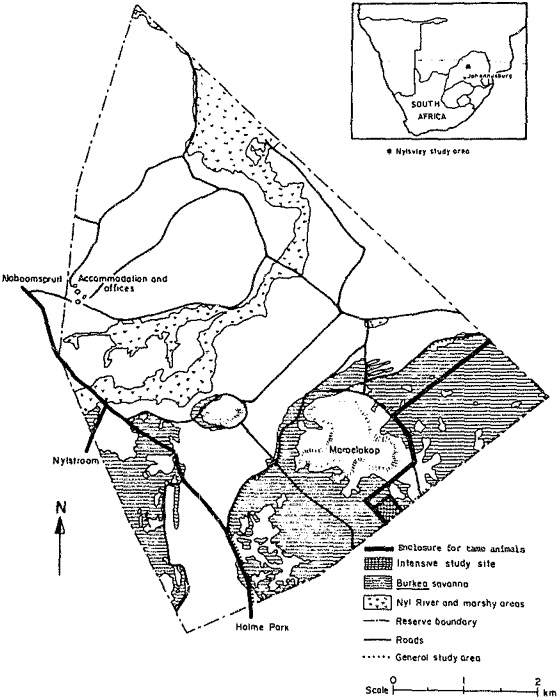


Figure 2.1. Nylsvley Nature Reserve and the Savanna Ecosystem Project Study Area.

savannas can be divided into two main groups. The broad leaf savannas which occur on dystrophic soils, and the microphyllous savannas which are found in more eutrophic areas. These two major savanna types may co-exist in a mosaic, as is found at Nylsvley, due to small scale differences in the soil nutrient status (Huntley & Walker 1982).

2.3. Geomorphology and Soils

The SASEP study area lies at 1100 m above sea level, sloping northwestwards to approximately 1085 m on the Nyl River floodplain. The topography is flat to gently sloping. The slope rarely exceeds two degrees.

The soils are moderately shallow to deep, well-drained and highly leached, non-calcareous, sandy soils of the Clovelly and Hutton forms derived from the sandstones, conglomerates and grits of the Waterberg system. Available phosphorus levels are generally 2-3 ppm, although small areas with enhanced nitrogen, phosphorus and potassium content, occur at sites thought to be previously occupied by native settlements (Harmse 1977).

2.4. Climate

The climate is typical of most savanna areas in South Africa. Meteorological records over the last 40 years indicate that the climate comprises a hot, wet season lasting from November until March during which 79% of the mean annual precipitation of 630 mm

Table 2.1. Monthly Rainfall (mm.) Measured at Nylsvley over the Period 1980 to 1983

Month	1980	1981	1982	1983
January	-	185.3	157.8	87.9
Febuary	-	33.7	54.2	47.0
March	-	41.2	36.6	105.5
April	-	23.3	48.9	53.1
May	0.0	2.9	17.5	2.6
June	0.0	0.0	0.0	13.4
July	0.0	0.9	4.6	0.3
August	0.0	12.8	0.0	15.7
September	54.9	13.0	4.0	0.0
October	18.1	34.7	46.6	28.9
November	155.5	68.2	39.9	230.4
December	67.8	43.5	92.7	50.1

falls. From late April to the end of A'.,ust it is mild and dry, with ground frosts occuring on appro'.imatly 20 days. While September and October are generally hot and dry. As in most savanna regions the rainfall is erratic and mid-summer droughts are frequent (Huntley 1978).

The annual precipitation during the time of this study was below average (Table 2.1.). From July to June the annual rainfall in the year 1980-81 was 583 mm. The following two years were drier, receiving just under 500 mm. In 1981 the first good rains fell in September. In the following two years the first significant rains did not fall until October, but more rain fell in April at the end of the wet season, thus slightly extending the season of plant growth.

2.5. Vegetation

The study area is located in an area of mixed, deciduous bushveld (Acocks 1954 Veld type 18, Blankenveld). The main plant community is Burkea africana - Eragrostis pallens deciduous broadleaf savanna woodland. This savanna shows similar floristic, physiognomic and faunal characteristics to the dystrophic savannas of the central and southern African plateaux. Nylsvley is situated at the southern limit of this savanna type.

The woody component of Burkea savanna comprises of clumps of trees of up to 12 m height interdispersed between grass and shrubs. The dominant trees are Burkea africana, Terminalia sericea, Ochna pulchra and Combretum molle, while the dominant shrubs are Grewia flavescens and Ochna pulchra (Coetzee et. al. 1977). The canopy cover of the woody component averages 27.5% (van Rooyen & Theron 1977).

Small patches of microphyllous Acacia short tree savanna occur on sites of abandoned native settlements where the soil is enriched particularly with phosphorus. This savanna is dominated by thorn trees of 2 - 6 m height, in particular Acacia nilotica, Acacia tortilis and Dichrostachys cinerea. The transition between the Acacia patches and the Burkea savanna is often marked by Scleryocarya caffra trees. The Acacia savanna is more open than the Burkea savanna, having a canopy cover of 15% (Coetzee et. al. 1977).

The field layer of the Burkea savanna is dominated by the grasses Eragrostis pallens and Digitaria eriantha in the open areas and Panicum maximum in the shaded areas. The field layer cover is 15 - 65% and the cover of leaf litter 5 - 10%. Eragrostis lehmanniana is the dominant grass in the Acacia savanna where the field layer cover varies from 25 - 95% (Coetzee et. al. 1977).

An indication of the plant species diversity is obtained from sampling in 1979 (Whittaker & Morris unpubl.). An average of twelve plant species per m2 was found in belt transects through Burkea savanna and only five species per m2 in the Acacia patches.

From aerial photographs taken in 1974 it is calculated that the *Acacia* savanna covers only 8% of the area in which this study was conducted.

2.6. Animal Populations

Prior to being declared a nature reserve the farm of Nylsvley was estimated to contain 150-500 impalas, and 40-100 kudus in addition to duikers, steenbok, 50-100 warthogs and 8 reedbuck (Coetzee et. al. 1977). Kudus and impalas have remained the most numerous species of ungulates in the reserve. In 1980 when this study began the reserve contained approximately 100 kudus and 700 impalas. Over the following three years the kudu population has remained fairly stable but the impalas have been reduced to 300 through culling. Species formerly present in the area were re-introduced to the reserve and the present ungulate population consists of 11 giraffe, and approximately 260 grazing ungulates including zebra, wildebeeste, roan antelope, waterbuck, reedbuck and tsessebe. Numerous duiker, steenbok and smaller herbivores also occur.

2.7. Management History

In the fifty years prior to becomming a provincial nature reserve in 1974 Nylsvley had been managed as a cattle ranch with 700-500 head of cattle. Up to 300 cattle were grazed in the study area for the four months of January to April. The presence of the highly poisonous woody geophyte, *Dichapetalum cymosum*, made longer grazing periods impractical. Cattle were also run in the study area during these months in 1975-1975 (Huntley 1978), and 200 head of cattle were introduced into the 213 ha enclosure for one month in March 1981 in order to remove the moribund grass which was constituting a fire hazard.

As a ranch Nylsvley was not burned intentionally. Accidental fires occurred at irregular intervals and it is estimated that approximately half the study area was burned once in five years (Coetzee et. al. 1977). Within the 213 ha enclosure the western half was burned in September 1978 and the remainder in 1979. Roadside fire breaks were burned every year, but other than this the enclosure was not burned during the study period.

CHAPTER 3.

THE REARING AND TAMING OF BROWSING UNGULATES FOR FEEDING STUDIES

3.1. Age and Origin of the Animals Used in this Study

Eight impala lambs, aged between two and ten days old, were captured at Nylsvley Nature Reserve in December 1979. Three impalas of similar age were brought in from nearby farmland. The group initially consisted of seven males and four females, but unfortunatly one male broke its neck in the fence when the group was panicked, probably by a stray dog in the reserve. One male impala had been raised from birth as a pet and was consequentially imprinted on humans. As a lamb he fled towards humans when frightened and directed his play behaviour towards them. However when unaware of the presence of humans he interacted apparently normally with the other impalas. Unfortunatly this animal and one other male died of injuries sustained while fighting with other impalas in March 1982 and October 1981 respectively.

The six kudus were acquired between April 1979 and July 1981. All but one were estimated to be about two months old on arrival. The first two calves came from the Nylsvley region. An injured male calf was brought in from a nearby farm in April 1979 having been mauled by dogs. This animal suffered the loss of an eye and extensive lacerations to the face and neck so was of no use for feeding observations. Instead he carried the radio-collar necessary for locating the group, as this slid up and down the neck of the animal and may have interfered with the natural feeding behaviour. A five month old female was caught at Nylsvley in April 1979. The kudus acquired later came from Transvaal bushveld areas. A female calf was purchased from a game farm at Thabazimbi in March 1981. Finally three calves, two males and a female, came from Loskop Dam Nature Reserve in July 1981.

Five female boer goats were purchased, when just weaned, from a nearby farm in July 1980. The boer goat is primarily a meat breed used by farmers in bushveld regions.

3.2. Housing

The animals were housed in single species groups in 8 x 12m pens lined with hessian and padded with thatching grass to prevent the animals from damaging themselves or being disturbed by activities outside the pens. Each pen contained a shed in which the animals were put at night. Four interconnecting pens were available and the animals were moved to a fresh pen every third day to prevent the build up of disease organisms, particularly coccidiosis, in the soil. Strict hygiene was observed at all times and no animals were lost due to disease.

3.3. Rearing and Weaning on to Plant Food

The animals received powdered baby milk enriched with vitamins. The impalas and the four younger kudus were bottle fed, while the injured calf and the oldest kudu drank their milk from buckets which were eventually hand held.

A continuous supply of cut branches of indigenous woody plants, hung on the pen walls, was always available to the animals and buckets of forbs were supplied. (Frost 1981). Once the animals had become tame enough to be guided in and out of the pens without stress they were allowed out in to a two hectare paddock of indigenous vegetation during the daytime. Taming to this level took one month for the impalas and two months for the kudus. Supplementary feeding was by "Epol" antelope cubes (see appendix 1 for composition) and fresh water was always available. The impalas received a dose of rumen fluid from a culled impala and to ensure that they had the microflora to digest the vegetation, the kudus were older when caught and were presumed to have been inocculated naturally. The impalas were fully weaned at six months and the kudus at eight months.

3.4. Training

The animals were subjected to human contact f several hours a day. Initially a technician sat quietly in the pen then, after two or three days, began to move around. Eventually the animals came to tolerate small groups of people walking around and talking in the pens. The kudu caught at five months old remained nervous of strangers, especially men. All the animals came readily to the sound of a few antelope cubes rattled in a bucket, the impalas also came to a voice call. Once weaned the animals were occasionally given a handful of antelope cubes to keep them tame, but no feeding was allowed for at least two days before their feeding wa. . ecorded.

Once weaned the animals were moved to a 213 hectare enclosure in the stud. 1. This enclosure was bounded by a ten foot wire fence, the lower half of which was made of mesh to prevent the tame impalas from getting out and wild animals from entering. This was not entirely sucessful so additional strands of wire were added. The fence also failed to isolate the kudus from the wild population as both tame and wild kudus occasin ly jumped over it. There was a four hectare enclosure within the main enclosure incorporating a 10 x 10 m hessian lined pen with a leopard-proof overnight shed for the goats. Two water dams were available, one within the four hectare enclosure and another just outside it. As in the reserve a salt lick was available for the animals (see appendix 2 for the mineral composition of the lick).

The impalas and goats were transported to the study area in June and July 1980 respectively. The impalas were transported by crate but the kudus had to be immobilised for the move. The oldest female and the injured male were transported in February 1981, the second female in September and the last three in November 1981. The animals were initially released into the four ha enclosure to ensure that they had not suffered any injury during the move. After two weeks the animals were released into the main enclosure. Prior to the onset of data collection the animals were followed in mock trials whilst feeding until they ignored the observers and learned to step over the string rather than becoming entangled in it.

3.5. The Experimental Animals at the Time of the Study

When data collection began the animals were all weaned and had been living freely in the study enclosure for at least two months. This ensured that they were familiar with the enclosure and that the rumen microflora was fully adapted to the diet (van Soest 1983)

At the initiation of the study in December 1980 the five female boer goats were 12 months old. These animals had no fear of humans and could be handled freely even while feeding. Following the loss of one goat to a leopard, only two months after the initiation of data collection, the goats were kept in a shed at night with a handful of antelope cubes to lure them inside.

The ten impalas were also 12 months old when first used for feeding observations. The group comprised four females and six males. Four of the impalas would feed from the hand and all were undisturbed when feeding by the presence of humans at a distance of two to three metres. If the observer came too close the impala would give a warning "hiccup" but did not stop feeding. One impala was imprinted on humans, seeking out their company in preference to that of impalas. Although the foraging patterns of this animal may have been influenced by his desire to remain close to the observer he was invaluable for observations on the fine details of feeding behaviour. The remainder of the group showed no social behaviour to people. They reacted normally to other animals. At the age of 18 months the four female impalas joined a group of wild impalas in the 213 hectare enclosure and were consequently lost to the project. They conceived during their first breeding season and sucessfully raised their young. On reaching maturity one of the tame males displaced the wild ram from the group of impalas including the tame females and became the dominant male. All the impalas have remained unafraid of humans and even two years after the cession of the field studies will leave the wild herd and come to me when called.

The kudus were not available for study until September 1981. Initially the group consisted of two females of 12 and 18 months old. These were joined three months later by two males and one female of ten months old. All the kudus ate from my hand and could be observed from a distance of two to five metres when feeding. The oldest female remained wary of the presence of humans while she was feeding and some days would constantly drift away from the observer. Similarly if the observer failed to see a kudu behind a bush and came too close the whole group would move away but soon resumed feeding. Like the impalas, the kudus remained tame throughout the study. Similarly they showed no social behaviour towards humans. During the breeding season the females bred with wild kudu bulls which jumped into the enclosure. The calves born subsequently were reared sucessfully by their mothers.

The goats, being domesticated animals, soon became completely tame and the only thing the observer had to beware of was getting so close as to restrict the goat's choise of movement in one direction.

3.6. Use of the Enclosure by the Animals

The kudu ranged over the whole of the enclosure. Their stocking density was 2.8 km-2 which is similar to that of the natural kudu population in the Nylsvley Nature Reserve.

In addition to the tame impalas there was a small herd of wild impalas in the enclosure. The stocking density of impalas was 10 km-2 in the enclosure and 13 km-2 in the reserve. Initially the tame animals used the whole enclosure but when they were 18 months old the females joined the wild herd and the young males tended to be restricted by the herd ram to an area of 30 ha. on the western side, although they still used the rest of the enclosure fairly frequently, especially in the late dry season.

The four goats restricted themselves to an area of 10 ha. around their overnight shed, rarely extending their range even in the dry season when they had depleted the preferred browse in their home area.

3.7. The Effect of Taming on the Food Selection of Wild Animals

An obvious question to be asked about the use of tame animals for feeding studies is how representative of the wild population are they? Studies on both livestock and hand-reared game species indicate that foraging behaviour is a combination of innate behaviour and learned responses (Arnold 1964 a & b, Leuthold 1971, Neff 1974, Frost 1981, Bartmann & Carpenter 1982).

The impalas used in this study were captured before they had any experience of browsing, but the kudus were between two and five months old so were already eating browse when caught.

At the age of two or three weeks the impalas were presented with branches of 48 species of indigenous browse plants to which their responses were recorded (Frost 1981). They rejected all the plants not eaten by the wild population at that time of year, plus four species which were edible, including Grewia flavescens which became one of their principal food plants when they were weaned. In the dry season, when the impalas were six months old, they began to eat many of the previously rejected species since the favoured browse was sparse. The same behaviour was seen in the wild population.

Leuthold (1971) found the same patterns with hand-reared lesser kudu and gerenuk. Both initially refused all the naturally rejected species plus a few others, some of which were important food plants to the wild animals. The gerenuk ate a few species eaten by the lesser kudu but not by wild gerenuk, indicating learning by imitation. The animals used in this study did not have older animals to imitate but were raised in single species groups so could not be influenced by the feeding behaviour of different species.

Preweaning experience of the vegetation has an important effect on food selection. Arnold (1964b) showed that grazing experience in the first three months of life affects the selection of unpalatable plants by sheep, but this effect is overcome in one month. Similarly pen reared lambs took one week to learn to graze as selectively as field reared lambs and 13 weeks to achieve a comparable intake rate (Arnold 1964a).

Bartmann and Carpenter (1982) cautioned that animals used for feeding studies must be preconditioned to the habitat. Mule deer in a novel habitat ate less species and showed more variability than deer of the same age which were raised in that area.

To allow for these factors the animals used in this study were always supplied with freshly cut branches of the local vegetation and buckets of forbs. Two months after capture they were allowed access to a two hectare paddock of indigenous vegetation during the day. The animals were transported to the study area when weaned and allowed two months to adapt to the vegetation and familiarise themselves with the area before feeding observations were taken.

Supplementary feeding by "Epol" antelope cubes was necessary when the animals were in the rearing pens and small quantities were occasionally given to the weaned animals to reinforce their tameness. Feeding was not allowed for at least two days before feeding observations were carried out, even though Reglin et. al. (1976) have shown that supplementary feeding had little effect on the selection of common species by mule deer.

Frequently the male animals used in feeding studies are castrated. This may enhance the safety of the researcher but such animals are not typical of the wild population. Consequently the male antelope used in this study were all left entire. No problems were encountered with these animals, although the imprinted male impala may have become a nuisance had he lived to full maturity.

Individual differences in food selection are frequently reported (Arnold 1964a, Willms & McLean 1978, Bartmann & Carpenter 1982). Therefore a minimum of five animals of each species was obtained for this study.

The use of sub-adult animals in this study may have had some effect on food selection as the wild population is typically a mixture of ages, but as the aim of this project is to identify the plant factors influencing diet selection by the three different animal species this fact that all the animals are sub-adult is, hopefully, not too serious.

The animals in the enclosure were stocked at similar densities to those in the reserve to ensure that they do not subsist only on the preferred food items but also suffer some nutritional stress in the dry season. A loss of body condition was observed in the tame animals during the late dry season indicating that, like the wild population, they were under some nutritional stress at this time of year.

Minor differences may occur in the feeding behaviour of animals in a small group rather than a herd due to less frequent social interations. If this does occur it will be more serious for the impalas and goats than the kudus which do not naturally occur in large herds.

CHAPTER 4.

PLANT SPECIES SELECTION BY BROWSING UNGULATES

4.1. *INTRODUCTION*

Herbivores often appear to be surrounded by a super-abundance of potential food. However much of this plant material is not suitable as food to the animals due to low nutrient contents, difficulty of access, and the presence of plant defence chemicals deleterious to the fitness of the herbivore. Hence the herbivore must be selective in its utilisation of plant material if it is to obtain an adequate diet.

The use of the various terms in feeding studies is presently rather flexible. To avoid further confusion these terms must be clearly defined as they will be interpreted in this study. The ABUNDANCE of a potential dietary component is defined as the total quantity of that component in the habitat, and is independent of the animal consumer. The AVAILABILITY of a component defines that portion of the total which is accessible to the consumer, e.g. within its height reach. The UTILISATION is the quantity of a component which is consumed by the animal in a fixed period of time. If dietary intake differs from availability in the relative proportions of components, SELECTION has occurred. PREFERENCE is a term reserved for selection by the animal and its active behavioural choice. It reflects the relative likelihood of a *component* being eaten if offered at the same time as others. In theory components can be ranked from most preferred, or favoured, to least preferred. REJECTED components are those which are never, or very rarely, eaten. Preference is frequently claimed to be independent of availability but is generally defined by reference to the choice made at equal availabilities. ACCEPTANCE measures the frequency with which a component is eaten if it is encountered. PALATABILITY refers to the characteristics or conditions of a food component influencing its likelihood of being eaten by the consumer (Heady 1964, Johnson 1980).

The interrelationships between animal populations and their food supplies are important in animal nutrition and ecosystem management as well as in theoretical ecology. Plants differ in their nutritional value to herbivores. Natural selection is assumed to ultimately favour those individual animals that select a diet that conveys the maximum net benefit (Lacher et. al. 1982). Such a diet must contain adequate nutrients and the minimum of deleterious plant secondary compounds. The patterns of food selection exhibited by herbivores control the contribution of a plant species to the nutrition of the animal.

The varying degrees of herbivory experienced by different plant species within a community may ultimately alter the species composition of that community by the suppression of heavily utilised food species. The patterns of food selection exhibited by a herbivore population can be placed in a functional model linking the habitat to population performance. Most theoretical models of foraging have been designed with carnivores in mind. For herbivores the pursuit and catching times are largely irrelevant, but there are constraints inherent in the time taken to digest the plant material due to the large quantities which must be processed in order to obtain a sufficient intake of nutrients. There is also more variation in the quality of the items making up the diet of herbivores than carnivores (Owen-Smith & Novellie 1982). With these differences in mind several models of herbivore foraging are available, all of which require a knowledge of the herbivores food preferences before they can be applied to natural systems.

Food selection by large generalist herbivores has been measured using a variety of techniques.

a. Dietary Proportions.

Studies on the relative proportions of plant species and parts in the diet reveal the contribution that different components make to the animal's nutrition. Principal foods are those two or three components which form the largest fraction of the diet (Petrides 1975). These components provide the bulk of the animal's nutritional intake. However species which are rare in the diet may provide some vital factor in the nutrition of the animal. A preferred food species is one which is relatively more abundant in the diet than it is in the available environment (Petrides 1975). The contribution a plant species makes to the overall diet of a herbivore is influenced by the availability of that species in the habitat. Highly preferred, but rare, species can only form a small part of the diet, while less preferred, but common, species can make a larger contribution to the diet. Henc a principal food species may be less preferred than many of the rarer species which are not abundant enough to rank highly in the diet (Petrides 1975).

b. Selectivity ratio.

The selectivity ratio, forage ratio, or electivity, is a measure of preference, whereby the use of food types (ri) in relation to their availability in the environment (pi) is measured. Foods that constitute a larger proportion of the diet than of the available food are said to be preferred, while those which are underrepresented in the diet relative to their availability in the environment are said to be avoided. A food is said to be eaten at random if its proportion in the diet equals its proportion in the environment (Petrides 1975, Pyke et. al. 1977, Lechowitz 1982).

The ideal selection ratio for herbivores must:-

i. include multiple food types,

ii. not be influenced by the abundance of other food types,

iii. have a symmetrical and finite scale centred on zero,

iv. change linearly over the full range of values for utilisation and availability.

v. be statistically testable,

vi. not be too sensitive to sampling errors.

No one thod of determining preference satisfies all these criteria (Cock 1978, Johnson 1980, Lechowitz 1982).

Many models of preferrence are limited to the two prey case. (Loehle & Rittenhouse 1982). Cock (1978) states that these models can be extended by pooling all prey types except type 1 into type 2, then treating as a 2 prey index. This is not tenable unless the pooled prey are all equally preferred (Loehle & Rittenhouse 1982). The forage ratio (Ei = ri/pi) (Ivlev 1961) takes a value of 1 for random feeding and differs asymmetrically from 1 to infinity for preferred foods and 0 to 1 for avoided items. The values can be made symmetrical by taking the logarithm of this index (Jacobs 1974). The forage ratio is easy to interpret in terms of whether an animal is selecting for or against a food item, but this is a statistical artifact. The values obtained by the forage ratio are dependant upon what one considers to be available (Straus 1979, Johnson 1980, Loehle & Rittenhouse 1982). Thus considering all the grass to be potentially available food for a browser means that all browse species become highly preferred. If grass is excluded the values for particular species change drastically. Hence the random feeding value of 1 is a statistical artifact with no behavioural meaning. Strictly quantitative comparisons between forage ratios derived from samples of differing relative abundance are inappropriate as the values obtained are influenced by the availability of other food types (Lechowitz 1982).

Chesson (1978) and Vanderploeg & Scavia (1979a) normalised Ivlev's forage ratio to overcome the problem of variation with relative abundance of other items in the sample. Their indices are however non-linear and symmetrical only in trials involving two food types. Again these indices are vulnerable to sampling errors for rare species, but they do allow comparison between samples (Lechowitz 1982).

Ivlev's (1961) electivity index Ei = (ri - pi)/(ri + pi) was designed to yield values between +1 and -1. This is an advantage in that it gives selection values between definite limits. However the extreme values of E cannot always be obtained. Deviations from the random model are symmetrical but not linear, so values are not proportional to the actual differences in preference indicated by the data (Petrides 1975). Since the maximum and minimum values depend on the relative abundance of food types the preference values calculated using this index for different food densities are not directly comparable (Landenberger 1968, Jacobs 1974). Rare food items and small sample sizes remain a problem. Large sample sizes are required but in heterogenous natural systems these may reveal even rarer species (Lechowitz 1982) .

Vanderploeg & Scavia (1979b) developed a relativised electivity index with a range of +1 to -1. Again the maximum values cannot be obtained and rare species are a problem. The index is markedly non-linear and asymmetrical, but is not affected by changes in the relative abundance of food types. This index is not amenable to parametric statistics but includes a measure of the deviation from non-selective feeding that makes rank order comparisons of electivity from diverse sites meaningful. These sites must however contain the same food types.

Although the various selection ratio indices give different values they still give the same rank order of preference. The selection ratio, in various forms, is the most widely used technique for measuring forage preferences, particularly of wild animals (McLean & Willms 1977, Monro 1979, Dunham 1980, Korfhage & Nelson 1980, Vangilder et. al. 1982).

Many studies have compared the proportion of a plant species in the environment with that in the diet of large mammals as represented by rumen or faecal samples (McLean & Willms 1977, Monro 1979, Dunham 1980, Korfhage & Nelson 1980, Vangilder et. al. 1982). However differential rates of digestion can cause inaccuracies in the estimations (Kessler et. al. 1981), particularly when faecal analysis is used (Jarman & Gwynne unpublished). Alternatively utilisation can be estimated from the feeding time then compared to the availability (Milton 1979, White & Trudell 1980, Glander 1981).

Estimating preference as being the ratio of the proportion of a plant species in the diet as compared to that in the environment can lead to inaccuracies as it incorporates both area, or patch, selection as well as food selection (Nudds 1980). Animals may select only from those plants within the range of its sensory capacities (Loehle & Rittenhouse 1982). Determination of resource availability in nature is beset by the fact that it may be impossible to measure it from the point of view of the animal under consideration (Jaenike 1980). Owen-Smith & Novellie (1982) avoided the effects of area selection by measuring availability as the standing crop density of plant species in the habitat volume scanned. This volume is the product of the distance moved in time, the effective path width and the maximum height reach of the animal.

c. Acceptance Value

The frequency with which an animal eats a food type when it is encountered gives an indication of the selection independent of the abundance of that food type in the environment. Difficulty is encountered in deciding which plants have been detected by the animals. Arnold (1966) showed with grazing sheep, that food items were detected primarily by smell and then by sight. For the measurement of the acceptability the plants available to the animals were estimated as being those within the neck reach of the animals. This avoids any assumptions about the animals foraging patterns and avoids arbitrary limits being placed on the animals sensory capacity to detect foods (Loehle & Rittenhouse 1982). Again problems are encountered with rare species which are only encountered infrequently. The acceptance values obtained for animal species with different encounter rates are not directly comparable, however the ranked values may be compared. Acceptance is related to utilisation in that an animal which eats mainly browse will have a greater acceptance value for woody plants than a mixed-feeder which also utilises grass thus bypassing many potentially edible browse plants while intent on grazing.

d. Duration of feeding on individual plants

Dietary contribution of a component is a compound of the frequency of acceptance and the duration of feeding on a food once accepted. The feeding duration is relatively independent of availability. The dietary importance of plant species to mule deer was calculated by measuring the number of bites taken from each plant encountered (Willms & McLean 1978, Bartmann & Carpenter 1982). Like the feeding duration this technique gives an estimation of the contribution of a food type to the diet.

e. Preference in choice situations.

Feeding trials using domestic livestock frequently employ confined animals. These are given a choice of two or more foods in known quantities. Hence the availability of each food can be precisely matched and the effect of other food types present can be excluded. This method is not often used for assessing the preferences of wild animals. Penned animals may be offered cut branches in cafeteria trials (Jarman & Gwynne unpublished, Tucker et. al. 1976, Frost 1980, Papageorgiou et. al. 1981, Sinclair et. al. 1982), or food put out for wild animals at times when natural foods are scarce (Bryant 1981).

No single measure of food preferences of herbivores represents all aspects of food selection. The comparative utilisation of grass and browse is discussed, since the degree to which the different animal species use these vegetation types may influence their selection of browse plants. Four methods of measuring for plant species selection were used. i. The proportion of feeding time was recorded. ii. From this the selection ratio was determined, using data collected by other workers on the abundance of available plant species in the habitat. iii. The frequency with which a plant species was eaten if encountered was recorded, together with iv. the duration of feeding on the plant. The results obtained using these four methods are compared and a composite picture of food selection by browsing ungulates is presented.

4.2. METHODS

The foraging behaviour of each animal species was observed for a minimum of six hours and a maximum of ten hours per month. FORAGING is defined as the time in which the animal is predominantly occupied with searching for and eating food. FEEDING refers to the actual consumption of the food. Every month the observations included each individual animal in order to reduce errors due to individual differences.

In each recording session a focal animal was followed, while foraging, for one hour. The species, size and leaf-age of each plant eaten and the duration of feeding on it was recorded verbally on a *Sony microcassette recorder* (Table 4.1.).

Simultaneously an assistant laid out a string along the path the animal took while feeding. Two reels of string were available, each measuring 1.5 Km. The string was secured with wire loops. The beginning and end of each period when the animal was actively engaged in feeding, within the recording session, was marked by blue and red plastic pegs, while yellow pegs indicated the turns made by the feeding animal as insurance against the string being broken by other animals.

Subsequently the feeding path was subdivided into quadrats of 1m long x the neck reach of the animal on each side of the string. In each quadrat details of the species, size and the leaf-age of

Table 4.1. Details recorded for each plant encountered by the animals.

i. Size

Size classes of woody plants.

Size Class	Maximum Height	Affected by:-
1	0.0 - 0.5 m	Fire, browsers, competition with grass
2	0.5 - 1.5 m	Fire and mammalian browsers
3	1.5 - 2.5 m	Kudus but too high for impalas and goats
4	above 2.5 m	Relatively free from mammalian browsing

Size classes of patches of individual forb species.

Patch Size	Number of plants in the patch
1	0 - 5 individuals
2	5 - 10 individuals
3	10 - 50 individuals
4	Covering all the 1m2 quadrat

ii. Phenology

Phenological classes for woody plants

Class	Phenology of leaves
N	New leaves not yet fully expanded.
Y	Young leaves, fully expanded but not yet fully hardened.
M	Mature, green leaves now hardened.
O	Old leaves with yellow marks or mottling.
D	Dried, partly brown leaves remaining on the plant.
F	Fallen leaf litter.

Phenological classes for forbs.

Class	Phenology
Y	Pre-flowering
M	Flowering
O	Post-flowering
D	Leaves dried

all the plant species available within the height reach of the animal were recorded. This gives a measure of the availability of each plant species to the animal during the period when its feeding behaviour was recorded. Plants encountered whilst the animal was running or walking rapidly with the head raised were not recorded, since at such times the animal was usually rejoining the other members of the herd and was not searching for food.

The reach of each animal species was measured directly from the animals while they were feeding, at least one member of each species being amenable to having the observer standing alongside it marking the twig just eaten from and the position of the hooves. The lateral reach of the animals was taken as the distance over which plants could be eaten by turning the neck whilst one forefoot remained stationary on the feeding path. This distance was 35 cm on either side of the string for the impalas and goats, and 50 cm for the kudus. The vertical reach was 150 cm for the impalas and goats. The goats are not as tall at the shoulder as the impalas but have the ability to stand on their hind legs. Roux (1968) also measured the browsing height of goats to be 150-157 cm. Subadult kudus could reach up to 200 cm.

The bite sizes and biting rates achieved by the animals for each plant species were record[illegible] the main observation sessions whenever possible w[illegible]urbing the animal under observation. Additional observatio[illegible] were also used. Bites were recorded sequentially on a microcassette recorder and described according to the plant part eaten, its phenological state, and in the case of woody shoots by the number of leaves taken in the bite. Subsequently samples of similar size and age were collected, dried and weighed. The intake rate was then calculated.

Initially it was attempted to randomise the hours and days of the month on which feeding data was collected, but this was not practical due to the difficulty in finding the animals in the enclosure, even with the radio-collar.

The majority of the feeding observations were taken in the morning. The animals seem to have two main feeding periods during the daylight hours occurring over the 2-3 hours after sunrise and before sunset. This was particularly evident in hot weather. Evening recordings proved impractical as the follow-up measurements of plant availability, which took from 2 to 4 hours to complete, had to be done promptly as markers left out in the veld overnight were frequently displaced by the animals. For the same reasons no night time recordings were taken.

The goats were studied for one year, from December 1980 to November 1981 inclusive. The kudus were not available during the first part of the project but were studied for the 12 months from September 1981 to August 1982. The impalas were observed throughout the whole period in order to monitor any differences in the feeding behaviour due to environmental differences. This was particularly important as a comparison was being made between the goats and kudus although they were not studied over the same time period.

From this method of data collection the comparative utilisation of grass and browse by the animals, and four measures of plant species selection were calculated.

The proportion of the total feeding time the animals spent eating grass and browse each month was compared. Browse material was split into woody and herbaceous browse. Leaf litter was considered separately but is a subsection of the woody browse category. Grass was taken to include the sedges since these are not abundant in the enclosure.

The differences in the proportion of each of these vegetation components in the monthly diet of the three animal species were tested for significance using the Mann-Whitney "U" test. Non parametric statistics were chosen as the daily variation in the proportion of each vegetation type was large, but it was the relative proportions of each component that was of interest.

In June and early July little data was collected from the kudus because of the presence of a wild male kudu in the tame group.

a. Dietary proportions.

The contribution of each browse species in the diets of the animals was estimated by the proportion of the feeding time spent eating that species during observation sessions. The dietary proportions of each plant species were compared over each of the four seasons using the Mann-Whitney "U" test.

b. Selectivity Ratio.

The species preference of the animals for woody plants was measured using the selectivity ratio. The selectivity ratio is the ratio between the proportion of a plant species in the diet and the proportion of that species available in the habitat.

Selectivity ratio = Proportion in diet. / Proportion in habitat.

The relative proportions of browse plants in the diet were calculated from the time spent feeding on browse corrected to a quantitative estimate by multiplying through by the intake rate for each species. The abundance of available woody plant foliage in the habitat was calculated from previous work by Rutherford (1979) and Witkowski (1980) in the height of the growing season. The above ground woody biomass of the Burkea savanna in the study area was measured by Rutherford (1979), his belt transects A and B were located within the enclosure in which the tame animals were kept. From these two transects the relative abundance of the eleven major woody plant species was obtained. The biomass available to the animals was calculated as being the biomass of leaves and the current years twigs of all shrubs below 2.5m plus 10% of the tree biomass.

Witkowski (1980) determined the total live canopy volume and that below 2.5 m for all woody plants, including the rarer species, in both the Burkea and Acacia savanna for the study area.

The relative proportions of Burkea and Acacia savanna within the enclosure in which the tame animals were studied, was calculated from pre-existing aerial photographs. Burkea savanna covered 92% of the enclosure, the remaining 8% being Acacia savanna.

The measurements of the relative biomass of available browse were calculated from the work of Rutherford (1979) for the common species occurring in Burkea savanna, and Witkowski (1980) for the Acacia savanna species and rare species. The relative biomass measurements for each species were adjusted according to the proportions of Acacia and Burkea savanna in the enclosure. Since the availability was measured only in peak growing season, the selectivity ratio could only be estimated for that season.

The species abundance and biomass of forb species was noticeably different each year, presumably as a result of variations in the rainfall patterns. Thus no previous information about the biomass of individual forb species was of use in determining the selectivity of the animals for forbs at the time of this study.

c. Acceptance value.

The frequency with which a plant species is eaten if encountered is a measure of selection that is not greatly influenced by the relative availability of that species to the animal. The acceptance value is the ratio of the number of individual woody plants, or patches of forbs eaten (see Table 4.1), divided by the number encountered within the neck reach of the animal along the path taken while feeding.

Acceptance value = number eaten / number encountered.

Chi-squared values from 2x2 contingency tables, with Yates correction for small numbers when necessary, were used to test for significant differences in the proportions of plant species which were accepted or rejected under different conditions. The results are expressed according to seasonal, rather than monthly, groupings in order to obtain a statistically acceptable encounter rate for the less abundant plant species.

d. Feeding duration.

The feeding duration is the time spent feeding on a plant once it has been encountered. The time, in seconds, spent feeding on individual plants was recorded. This included the time taken to pluck, chew and swallow the food. Occasions when an animal paused to observe its surroundings then continued to eat the same plant, or a neighbouring plant of the same species, were classified as a single feeding duration. When multiplied through by the intake rate a quantitative assessment of the amount of foliage consumed at one time can be obtained. This gives a measurement of preference without reference to the avaliability of the plant species in the habitat, if it is assumed that the animal will eat more of a preferred plant at one time than of a less preferred plant.

4.3. RESULTS

4.3.1. The Dietary Composition of Kudus, Impalas and Goats in Terms of Vegetation Components

i. Kudus

The diet of kudus consisted predominantly of woody plant leaves and shoots, an average of 60 ± 12% of the feeding time being devoted to this food source throughout the year. The utilisation of woody browse was at a maximum in the late dry season, forming 67 ± 3% of the diet (Fig. 4.1.i.)

Forbs were of less importance than woody plants, accounting for 20 ± 3% of the diet in the early growing season, decreasing to 10 ± 3% in the late dry season. Grass was not an important source of food to the kudus, constituting only 7 ± 2% of the diet as a year round average. The main species of grass eaten was Panicum maximum which grows under the shade of trees and is favoured by many animals.

The kudu made limited use of fallen leaves as a dry season food source, taking mainly Strychnos cocculoides and the large leaves of Combretum zeyheri when other food was scarce during the last two months of the dry season.

Fruit was actively sought out when available. The large fruits of Sclerocarya caffra and Strychnos spp. were eaten in the growing season, while in the early dry season the animals ate the abundant indehiscent pods of Acacia tortilis and Acacia nilotica. Together with Grewia flavescens berries these formed 24 $\pm$ 95% of their dry season diet.

The flowers of early flowering trees like Dombeya rotundifolia and occasionally Sclerocarya caffra and Ochna pulchra were eaten at the very end of the dry season. The twigs of Ochna pulchra bearing buds were also occasionally eaten just before the period of new leaf flush.

ii. Goats

Woody browse was also the most important dietary component for the goats, averaging 44 $\pm$ 5% of the year round diet. After the first flush of new leaves the use of woody browse decreased through the early growing season, then once again increased in January to become the most important part of the diet, occupying almost 80% of the feeding time (Fig. 4.1.ii.). The time spent feeding on woody plants then steadily decreased down to 21 $\pm$ 75 in May, then increased again throughout the remainder of the dry season.

Forbs were not of great importance in the diet of the goats in the early growing season and late dry season, but constituted 22 $\pm$ 9% of the feeding time in February and March. The maximum usage of grass by goats occurred in December when almost 50% of the feeding time was devoted to this food source. The use of grass then

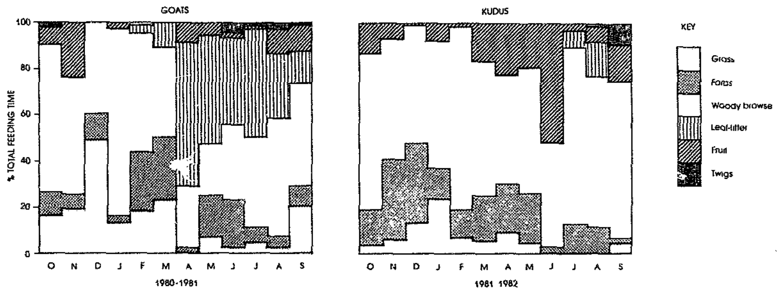


Fig 4.1. The Monthly Composition of the Diets of Browsing Ungulates.

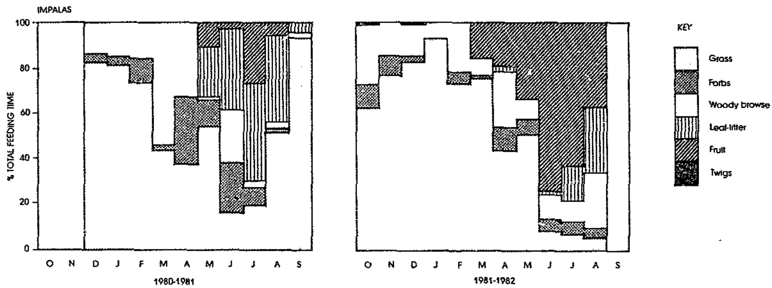


Fig 4.1. The Monthly Composition of the Diets of Browsing Ungulates.

declined to less than 1% in April and remained low until the regrowth of green grass in September.

In the dry season fallun leaves were an exedingly important source of food to the goats. They began using leaf-litter in late February and by April 62 ± 4% of their diet consisted of fallen leaves.

Fruit were eaten when available, but never became a major part of the diet. Twigs of Ochna pulchra and Dombeya rotundifolia were occasionally eaten in the late dry season when the buds were swelling.

iii. Impalas

The proportions of the components making up the diets of the impalas in each month were similar over both years studied. The main food of impalas was green grass (Fig 4.1.iii.). This accounted for 73 ± 4% of the growing season diet on average, but reached 90% when the new season's grass flushed on the burned fire breaks in September. In the dry season the availability of green grass decreased until in the second year the impalas spent only 5-10% of their time feeding on grass, carefully selecting the few remaining green leaves.

The use of woody plant and forbs by impalas was low and inconsistent. Forbs provided less than 10% of the diet during the growing season and 15-20% in the dry season. An average of 20 ± 6%

of the feeding time was spent eating woody plants from the time of new leaf flush to leaf fall, while in the late dry season the impalas ate less from the trees and bushes but ate the fallen leaves. Leaf-litter was an important dry season food resource for these animals. In 1981, from the month of May, the use of fallen leaves of palatable trees increased until 40% of the diet comprised leaf-litter in July. Fallen leaves were not as important a food source in the following year and were only eaten at the very end of the dry season. This was due to the abundance of the preferred dry season food, Acacia pods. In the dry season of 1982 there was a particularly good crop of Acacia pods. The pods fell from the trees throughout the early dry season providing a continuous supply of food. This peaked in June when the impalas spent 75 $\pm$ 5% of their time feeding on pods, particularly those of Acacia tortilis, and on Grewia flavescens berries. The use of fruit and leaf-litter terminated abruptly as soon as new grass appeared on the burned areas.

iv. A Comparison of the Dietary Compositions of Impalas in Two Consecutive Years

A comparison of the feeding behaviour of the impalas over the two years of the study revealed few differences in the proportions of the major food types in the diet. In 1982 the flush of new grass on the burns was later; as a consequence the diet of the impalas in August of this year contained significantly less grass than in the previous year, but more woody browse (Table 4.2.a.). Less woody browse was eaten in March 1981 than in the same month in the

Table 4.2.a. Comparison of the Dietary Proportions of the Major Food Types by Impalas in 1980-1 and 1981-2, Values of the Wilcoxon "U" Statistic.

		Grass		Woody browse		Forbs		Leaf-litter		Fruit	
Month	"U"	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981
October	-	-	-	-	-	-	-	-	-	-	-
November	-	-	-	-	-	-	-	-	-	-	-
December	10	29.5	24.5	26.5	27.5	32.0	22.0	13.5	40.5	-	-
January	5	14.0	21.0	11.0	25.0	18.5	16.5	-	-	21.0	15.0
Febuary	5	17.0	18.0	12.5	22.5	29.0	7.0	-	-	2.0	18.0
March	0	3.0	9.0	15.0	0.0 *	7.0	8.0	-	-	2.0	18.0
April	2	5.0	19.0	16.5	7.5	22.0	2.0 *	8.0	16.0	0.0	24.0 *
May	10	27.0	29.0	17.0	39.0	35.5	13.5	44.0	12.0	9.5	46.5 *
June	8	36.5	12.5	31.0	18.0	31.0	18.0	49.0	0.0 *	0.0	49.0 *
July	8	33.0	16.0	12.0	37.0	34.5	14.5	40.0	9.0	12.0	37.0
August	10	48.5	5.5 *	1.0	53.0 *	12.0	42.0	17.0	37.0	12.0	36.0
September	-	-	-	-	-	-	-	-	-	-	-

(* Significantly Different : $P < 0.05$)

Table 4.2.a. Comparison of the Dietary Proportions of the Major Food Types by Impalas in 1980-1 and 1981-2, Values of the Wilcoxon "U" Statistic.

		Grass		Woody browse		Forbs		Leaf-litter		Fruit	
Month	"U"	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981
October	-	-	-	-	-	-	-	-	-	-	-
November	-	-	-	-	-	-	-	-	-	-	-
December	10	29.5	24.5	26.5	27.5	32.0	22.0	13.5	40.5	-	-
January	5	14.0	21.0	11.0	25.0	18.5	16.5	-	-	21.0	15.0
Febuary	5	17.0	18.0	12.5	22.5	29.0	7.0	-	-	2.0	18.0
March	0	3.0	9.0	15.0	0.0 *	7.0	8.0	-	-	2.0	18.0
April	2	5.0	19.0	16.5	7.5	22.0	2.0 *	8.0	16.0	0.0	24.0 *
May	10	27.0	29.0	17.0	39.0	35.5	13.5	44.0	12.0	9.5	46.5 *
June	8	36.5	12.5	31.0	18.0	31.0	18.0	49.0	0.0 *	0.0	49.0 *
July	8	33.0	16.0	12.0	37.0	34.5	14.5	40.0	9.0	12.0	37.0
August	10	48.5	5.5 *	1.0	53.0 *	12.0	42.0	17.0	37.0	12.0	36.0
September	-	-	-	-	-	-	-	-	-	-	-

(* Significantly Different : $P < 0.05$)

Table 4.2.b. Comparison of the Dietary Proportions of the Major Food Types by Kudus and Impalas in the Year 1981-1982, Values of the Wilcoxon "U" Statistic.

		Grass		Woody browse		Forbs		Leaf-litter		Fruit	
Month	"U"	kudus	impalas	kudus	impalas	kudus	impalas	kudus	impalas	kudus	impalas
October	3	0.0	30.0 *	28.5	1.5 *	19.0	11.[illegible]	18.0	12.0	21.0	9.0
November	3	0.0	30.0 *	26.0	4.0	27.0	3.0 *	18.0	12.0	25.0	5.0
December	10	0.0	54.0 *	48.0	0.0 *	50.0	4.0 *	13.5	40.5	33.0	21.0
January	5	1.0	41.0 *	35.5	0.5 *	36.0	0.0 *	15.0	12.0	21.0	15.0
Febuary	6	0.0	40.0 *	40.0	0.0 *	35.0	5.0 *	-	-	25.0	15.0
March	8	1.0	39.0 *	45.5	14.5	38.0	12.0	-	-	22.0	18.0
April	8	0.0	48.0 *	37.0	11.0	39.5	8.5	16.0	32.0	18.5	29.5
May	6	5.0	37.0 *	42.0	0.0 *	9.0	33.0	18.0	24.0	8.0	34.0
June	-	2.0	12.0	10.0	4.0	6.5	7.5	6.0	8.0	5.0	9.0
July	12	9.0	54.0 *	63.0	0.0 *	41.5	21.5	24.0	39.0	2.0	54.0 *
August	15	12.0	60.0	61.0	11.0 *	58.0	14.0 *	12.5	59.5	17.0	47.0
September	2	0.0	25.0 *	25.0	0.0 *	22.5	2.5	7.5	17.5	25.0	0.0 *

(* Significantly Different : $P < 0.05$)

Table 4.2.c. Comparison of the Dietary Proportions of the Major Food Types by Goats and Impalas in the Year 1980-1981, Values of the Wilcoxon "U" Statistic.

		Grass		Woody browse		Forbs		Leaf-litter		Fruit	
Month	"U"	goats	impalas	goats	impalas	goats	impalas	goats	impalas	goats	impalas
October	3	0.0	30.0 *	30.0	0.0 *	21.0	9.0	29.0	1.0 *	24.0	6.0
November	3	0.0	30.0 *	30.0	0.0 *	15.0	15.0	25.5	4.5	27.5	2.5 *
December	7	0.0	45.0 *	44.5	0.5 *	32.0	13.0	-	-	-	-
January	8	15.0	25.0	41.0	7.0 *	17.0	31.0	-	-	27.0	21.0
Febuary	5	0.0	35.0 *	27.0	8.0	29.5	5.5	21.0	24.0	21.0	14.0
March	-	7.0	5.0	1.5	10.5	11.0	1.0	12.0	4.0	10.0	6.0
April	1	0.0	20.0 *	6.0	14.0	0.0	20.0 *	20.0	0.0 *	20.0	0.0 *
May	10	9.5	46.5 *	56.0	0.0 *	21.5	27.5	22.0	34.0	20.5	35.5
June	6	8.5	33.5	33.0	9.0	26.5	15.5	15.5	26.5	20.0	22.0
July	10	9.0	47.0 *	56.0	0.0 *	23.0	33.0	26.0	30.0	12.5	43.5
August	5	5.0	31.0 *	36.0	0.0 *	26.5	9.5	14.0	22.0	31.0	5.0 *
September	3	0.0	30.0 *	30.0	0.0 *	25.0	5.0	15.0	5.0	27.5	2.5 *

(* Significantly Different : $P < 0.05$)

Table 4.2.d. Comparison of the Dietary Proportions of the Major Food Types by Goats in 1980-1 and Kudus in 1981-2, Values of the Wilcoxon "U" Statistic.

		Grass		Woody browse		Forbs		Leaf-litter		Fruit	
Month	"U"	goats	kudus	goats	kudus	goats	kudus	goats	kudus	goats	kudus
October	5	31.5	4.5 *	17.5	18.5	15.0	21.0	36.0	0.0 *	22.5	13.5
November	5	27.5	8.5	14.0	22.0	0.0	36.0 *	33.0	3.0 *	11.0	25.0
December	7	41.0	4.0 *	11.5	28.5	12.0	33.0	-	-	17.5	27.5
January	8	21.5	26.5	2.0	46.0 *	4.0	44.0 *	-	-	19.0	29.0
Febuary	6	8.0	32.0	32.0	8.0	9.0	31.0	24.0	16.0	18.0	22.0
March	5	35.0	5.0 *	12.5	27.5	25.5	14.5	30.0	10.0	10.5	29.5
April	6	0.0	40.0 *	8.0	32.0	1.0	39.0 *	40.0	0.0 *	20.0	20.0
May	6	30.5	11.5	4.0	38.0 *	16.5	22.5	42.0	0.0 *	9.5	32.5
June	-	9.0	13.0	6.0	6.0	11.5	0.5	11.0	1.0	0.0	12.0
July	15	58.5	13.5 *	6.0	66.0 *	23.0	49.0	58.0	14.0 *	33.0	31.0
August	8	44.0	4.0 *	20.0	28.0	10.5	37.5	42.0	6.0 *	17.0	47.5
September	3	25.5	4.5	7.5	22.5	21.0	9.0	30.0	0.0 *	12.0	18.0

(* Significantly Different : $P < 0.05$)

following year. In 1982 the crop of Acacia pods was very good. From April until June of this year the impalas spent much more time feeding on these pods than in the previous year. Less leaf-litter was eaten in June and less herbaceous browse in April of 1982 than in 1981, presumably due to the increased time spent eating Acacia pods.

v. Comparison between the Animal Species

A month by month comparison of the dietary composition of kudus, impalas, and goats, at Nylsvley shows that the impalas ate a significantly greater proportion of grass than the kudus in all months of the year, except June and August when little green grass was available (Table 4.2.b.). They also ate more grass than the goats for the nine months of the year excluding January, March and June (Table 4.2.c.). The goats grazed significantly more than the kudus for five months of the year, only in April did the kudus eat significantly more grass than the goats (Table 4.2.d.).

The proportion of woody plants in the diet of the impalas was significantly less than that of the kudus throughout most of the year and less than the goats in the late dry and early growing seasons. The kudus made significantly greater use of forbs than the impalas in the growing season and than the goats in November, January and April. Leaf-litter was significantly more important to the goats than the kudus throughout the dry season and the early part of the growing season, the kudus preferring to obtain their browse from leaves remaining on the trees and shrubs. The goats also spent a significantly greater proportion of their feeding time eating fallen leaves than did the impalas from April to July.

There was no significant difference in the proportion of fruit in the diets of kudus and goats. In 1981 the goats ate significantly more fruit than the impalas in April and from August to November. The impalas ate significantly more fruit than the kudus in July 1982 but this pattern was reversed in September.

4.3.2. Plant Species Selection: Dietary Proportions

a. Woody Plants

The proportion of the total feeding time in each observation session that was occupied by individual plant species was highly variable. This was due to the heterogeneity of the vegetation and the limited number of food types which could be consumed in one hour. Frequently a plant species was not eaten within the observation period so scored a value of zero. This resulted in a high degree of variation and hence a poor statistical estimation of the species composition of the diet.

i. Kudus

G. flavescens made up the greatest proportion of the diet of the kudus during the growing and early dry seasons, when it formed approximatly 20% of the total feeding time and accounted for 40%

of the time spent browsing (Table 4.3.i.). Dichrostachys cinerea was also an important source of food in the growing season particularly from February to April when it occupied 20% of the browsing time.

In the early dry season from April to June G. flavescens continued to dominate the browse diet of the kudus but overall this species contributed a significantly smaller proportion to the total diet than in the growing season. D. cinerea and Vitex rehmannii were also favoured in the early dry season. These species are deciduous, losing their leaves in the latter half of the dry season.

The evergreen Strychnos pungens was a major dietary component in the late dry season from July to September, being eaten significantly more in this season than at any other time of year. The dead leaves of the deciduous species C. zeyheri and G. flavescens which remained on the branches were also eaten. The use of several evergreen species increased, and some plants such as the "thin-leaved" evergreens Pappea capensis and Rhus leptodictya developed distinct browse lines.

In September the new leaves of Diospyros lycioides and O. pulchra flushed out in advance of most other species and were readily eaten by the kudus. The new leaves of Burkea africana and Lannea edulis, which emerged in the following month, were also readily eaten. Both O. pulchra and B. africana leaves were ignored once they had matured. A second flush of O. pulchra leaves

Table 4.3. The Proportion of the Browsing Time (%) Spent *Feeding on Leaves and Shoots* of Woody Plant Species.

1. Kudus

Species	Early Growing Season n = 3			Late Growing Season n = 3			Early Dry Season n = 3			Late Dry Season n = 3		
	Mean	SE	Rank	Mean	SE	Rank	Mean	SE	Rank	Mean	SE	Rank
Species Selected for Chemical Analysis												
Acacia nilotica	0.07±	0.07	[illegible]	-	-	-	0.65±	0.48	17	0.72±	0.98	19.
Acacia tortilis	-	-	-	0.36±	0.20	20	1.42±	1.23	11	0.01±	0.01	31
Burkea africana	5.17±	2.55	7	3.80±	1.66	4	1.31±	1.14	12	0.40±	0.13	22.
Combretum molle	2.48±	1.84	10	0.90±	0.29	10	1.65±	1.65	10	2.93±	2.03	11
Dichrostachys cinerea	8.96±	4.27	2	25.39±	9.50	2	15.00±	11.74	2	0.13±	0.13	28.
Dombeya rotundifolia	2.02±	1.58	13	0.20±	0.17	22	0.01±	0.01	28	2.00±	1.09	10
Euclea natalensis	0.10±	0.10	23	-	-	-	2.25±	2.25	6	4.04±	1.05	7
Grewia flavescens	34.62±	6.47	1	38.83±	3.51	1	45.49±	10.99	1	8.22±	5.24	5
Ochna pulchra	6.63±	2.30	5	13.88±	12.39	3	0.15±	0.15	26	13.15±	12.82	3
Peltophorum africanum	-	-	-	-	-	-	-	-	-	-	-	-
Rhus leptodictya	0.17±	0.14	27	0.53±	0.53	15.5	1.91±	1.10	19	3.18±	1.60	10
Strychnos pungens	7.30±	5.59	3	0.13±	0.10	23.5	0.27±	0.23	20.5	16.74±	8.74	1
Terminalia sericea	0.29±	0.07	23	0.82±	0.30	11.5	0.31±	0.29	18	2.51±	2.10	13
Vitex rehmannii	5.50±	3.83	6	2.76±	1.24	7	9.84±	5.53	3	2.22±	0.02	14
Other Species												
Acacia burkei	0.12±	0.12	20	-	-	-	-	-	-	2.53±	2.50	12
Acacia caffra	1.20±	0.79	18	-	-	-	-	-	-	-	-	-
Acacia hebeclada	-	-	-	0.04±	0.04	26.5	-	-	-	-	-	-
Acacia karoo	0.83±	0.56	19	0.18±	0.10	25	1.69±	0.64	9	0.84±	0.84	18
Barleria bremekampii	0.05±	[illegible]	[illegible]	-	-	-	-	-	-	-	-	-
Bequartiodendron magalismontanum	-	-	-	-	-	-	-	-	-	-	-	-
Bridelia mollis	[illegible]	[illegible]	[illegible]	-	-	-	-	-	-	-	-	-
Canthium gilfillanii	-	-	-	-	-	-	0.20±	0.20	24	0.68±	0.68	20
Carissa bispinosa	0.10±	0.10	29	-	-	-	-	-	-	2.03±	1.69	15
Cassine transvaalensis	0.05±	0.05	33	-	-	-	-	-	-	0.15±	0.15	28
Combretum apiculatum	0.19±	0.19	25.5	3.24±	1.74	5	0.10±	0.10	27	-	-	-

Table 4.3. Continued. . .

Combretum zeyheri	7.17±	3.15	4	0.53±	0.27	15.5	1.11±	1.11	13	13.33±	8.92	2
Croton gratissimus	-	-	-	-	-	-	1.06±	1.06	14	-	-	-
Dichapetalum cymosum	-	-	-	-	-	-	-	-	-	-	-	-
Diospyros lycioides	1.30±	0.24	17	3.62±	2.16	6	5.47±	2.25	4	10.44±	10.44	4
Ehretia rigida	2.69±	2.26	9	0.60±	0.58	14	-	-	-	0.54±	0.27	21
Erythrococca menyharthii	0.24±	0.24	24	0.37±	0.24	19	0.32±	0.32	18	0.29±	0.18	25.5
Euclea crispa	0.03±	0.03	38	-	-	-	-	-	-	0.30±	0.30	27
Euclea undulata	0.19±	0.10	25.5	-	-	-	-	-	-	3.38±	3.27	8
Grewia bicolor	1.54±	0.82	15	-	-	-	-	-	-	0.10±	0.08	29
Grewia flava	0.03±	0.03	38	-	-	-	-	-	-	-	-	-
Grewia monticola	0.05±	0.05	33	-	-	-	-	-	-	3.78±	3.02	9
Lannea discolor	0.05±	0.05	33	1.09±	1.09	9	-	-	-	-	-	-
Lannea edulis	1.45±	0.74	16	0.47±	0.26	18	0.24±	0.24	22	-	-	-
Maytenus tenuispina	-	-	-	1.19±	0.66	8	0.27±	0.27	20.5	0.35±	0.35	23
Mundulea sericea	-	-	-	-	-	-	-	-	-	-	-	-
Ozoroa paniculosa	0.05±	0.05	33	-	-	-	0.23±	0.23	23	0.34±	0.19	24
Pappea *capensis*	0.76±	0.76	20	-	-	-	-	-	-	4.54±	2.18	6
Protea welwitschii	-	-	-	0.04±	0.04	26.5	-	-	-	-	-	-
Pseudolachnostylis maprounifolia	0.75±	0.75	21	0.71±	0.71	13	-	-	-	-	-	-
Pygmaeothamnus zeyheri	-	-	-	-	-	-	-	-	-	-	-	-
Rhus pyroides	0.56±	0.23	27	0.31±	0.22	21	0.78±	0.47	16	-	-	-
Sclerocarya caffra	0.04±	0.04	36	-	-	-	-	-	-	-	-	-
Securidaca longipedunculata	2.70±	1.05	8	0.82±	0.72	11.5	0.84±	0.75	15	0.02±	0.02	30
Securinega virosa	-	-	-	-	-	-	-	-	-	-	-	-
Strychnos cocculoides	1.94+	0.74	14	0.39±	0.21	17	0.07±	0.07	28	-	-	-
Strychnos *madagascariensis*	-	-	-	-	-	-	-	-	-	-	-	-
Tarchonanthus camphoratus	-	-	-	-	-	-	-	-	-	-	-	-
Vitex mombassae	-	-	-	-	-	-	0.21+	0.21	24	-	-	-
Vangueria infaustra	-	-	-	-	-	-	-	-	-	-	-	-
Ximenia caffra	-	-	-	-	-	-	4.85±	4.85	5	1.17±	0.60	17
Ziziphus mucronata	2.26+	0.85	11	0.13±	0.13	23.5	2.23+	2.16	7	0.29±	0.15	25.5

(*Standard error* calculated on a monthly basis in order to give equal weighting to each month)

Table 4.3. The Proportion of the Browsing Time (%) Spent Feeding on Leaves and Shoots of Woody Plant Species.

ii. Impalas

Species	Early Growing Season n = 4			Late Growing Season n = 6			Early Dry Season n = 6			Late Dry Season n = 5		
	Mean	SE	Rank	Mean	SE	Rank	Mean	SE	Rank	Mean	SE	Rank
Species Selected for Chemical Analysis												
Acacia nilotica	3.57±	2.16	9	10.80±	3.53	3	0.72±	7.30	4	-	-	-
Acacia tortilis	0.10±	0.06	29.5	5.21±	5.07	4	1.55±	1.26	11	-	-	-
Burkea africana	0.60±	0.43	20	0.25±	0.25	18.5	-	-	-	-	-	-
Combretum molle	3.22±	1.81	10	4.57±	2.29	5	4.22±	2.59	5	6.70±	3.43	7
Dichrostachys cinerea	15.22±	5.35	2	33.62±	17.90	1	23.05±	12.25	2	0.41±	0.41	14
Dombeya rotundifolia	0.10±	0.06	29.5	-	-	-	-	-	-	0.33±	0.33	16
Euclea natalensis	0.79±	0.79	18	-	-	-	-	-	-	12.90±	4.55	3
Grewia flavescens	30.88±	14.16	1	30.39±	14.53	2	23.73±	10.14	1	14.06±	9.70	2
Ochna pulchra	4.54±	3.89	6	1.87±	1.37	9	-	-	-	0.22±	0.22	18
Peltophorum africanum	0.41±	0.24	23	0.30±	0.30	17	0.29±	0.29	16	3.93±	3.68	8
Rhus leptodictya	1.06±	0.59	15	0.32±	0.25	15	0.98±	0.36	14	0.93±	0.52	11
Strychnos pungens	3.63±	0.87	8	0.08±	0.06	22	1.66±	1.15	10	8.18±	5.14	5
Terminalia sericea	1.80±	1.05	11	3.02±	1.06	7	1.39±	1.31	12	8.55±	8.55	4
Vitex rehmannii	0.59±	0.30	21	0.09±	0.09	21	2.40±	1.25	7	2.35±	1.59	9
Other Species												
Acacia burkei	9.23±	5.92	3	0.05±	0.05	24	-	-	-	-	-	-
Acacia caffra	-	-	-	-	-	-	-	-	-	-	-	-
Acacia hebeclada	-	-	-	-	-	-	-	-	-	-	-	-
Acacia karoo	0.28±	0.20	26	-	-	-	0.11±	0.11	20.5	-	-	-
Barleria bremekampii	-	-	-	-	-	-	-	-	-	-	-	-
Bequartiodendron magalismontanum	-	-	-	-	-	-	-	-	-	-	-	-
Bridelia mollis	-	-	-	-	-	-	0.11±	0.11	20.5	-	-	-
Canthium gilfillanii	0.63±	0.63	19	0.25±	0.25	18.5	-	-	-	-	-	-
Carissa bispinosa	5.43±	3.79	5	-	-	-	0.25±	0.25	17	6.86±	4.89	6
Cassine transvaalensis	-	-	-	0.06±	0.06	23	-	-	-	-	-	-
Combretum apiculatum	0.29±	0.29	25	-	-	-	1.21±	1.21	13	-	-	-

Table 4.3. *Continued. . .*

Combretum zeyheri	-	-	-	-	-	-	-	-	-	2.22±	2.12	18
Croton *gratissimus*	-	-	-	-	-	-	-	-	-	-	-	-
Dichapetalum cymosum	-	-	-	-	-	-	-	-	-	-	-	-
Diospyros lycioides	1.76±	1.21	13	-	-	-	0.12±	0.12	19	0.33±	0.33	16
Ehretia *rigida*	0.53±	0.30	22	0.98±	0.98	10	2.08±	2.08	8	0.33±	0.33	16
Erythrococca menyharthii	5.54±	2.83	4	3.88±	1.04	6	2.07±	2.07	9	-	-	-
Euclea crispa	-	-	-	-	-	-	-	-	-	-	-	-
Euclea undulata	1.79±	1.65	12	-	-	-	11.48±	9.11	3	30.16±	21.51	1
Grewia bicolor	-	-	-	-	-	-	0.07±	0.07	22	0.04±	0.04	21
Grewia flava	0.05±	0.05	33	-	-	-	-	-	-	-	-	-
Grewia monticola	0.36±	0.28	24	0.31±	0.31	16	-	-	-	0.65±	0.65	12
Lannea discolor	4.10±	2.15	7	0.33±	0.33	14	-	-	-	-	-	-
Lannea edulis	0.87±	0.87	16	-	-	-	-	-	-	-	-	-
Maytenus tenuispina	1.27±	0.66	14	0.16±	0.16	20	-	-	-	-	-	-
Mundulea sericea	-	-	-	-	-	-	-	-	-	-	-	-
Ozoroa paniculosa	0.23±	0.23	27	-	-	-	-	-	-	-	-	-
Pappea capensis	-	-	-	-	-	-	0. [illegible]	0.03	24	-	-	-
Protea welwitschii	-	-	-	-	-	-	-	-	-	-	-	-
Pseudolachnostylis *maprouneifolia*	-	-	-	-	-	-	-	-	-	-	-	-
Pygmaeothamnus zeyheri	-	-	-	-	-	-	-	-	-	-	-	-
Rhus pyroides	0.07±	0.07	32	0.40±	0.31	11	0.53±	0.53	15	-	-	-
Sclerocarya caffra	-	-	-	0.43±	0.24	12	-	-	-	-	-	-
Securidaca longipedunculata	0.81±	0.34	17	2.22±	2.22	8	2.91±	2.83	6	0.43±	0.43	13
Securinega virosa	-	-	-	-	-	-	0.06±	0.06	23	-	-	-
Strychnos cocculoides	0.08±	0.08	31	-	-	-	-	-	-	-	-	-
Strychnos madagascariensis	-	-	-	-	-	-	-	-	-	-	-	-
Tarchonanthus camphoratus	-	-	-	-	-	-	-	-	-	-	-	-
Vitex mombassae	-	-	-	-	-	-	-	-	-	-	-	-
Vangueria infaustra	-	-	-	-	-	-	-	-	-	-	-	-
Ximenia caffra	-	-	-	-	-	-	-	-	-	-	-	-
Ziziphus mucronata	0.21±	0.11	27	0.35±	0.35	13	0.23±	0.23	18	0.14±	0.14	20

(Standard error calculated on a monthly basis in order to give equal weighting to each month)

Table 4.3. The Proportion of the Browsing Time (%) Spent Feeding on Leaves and Shoots of Woody *Plant Species.*

iii. Goats

Species	Early Growing Season n = 3			Late Growing Season n = 3			Early Dry Season n = 3			Late Dry Season n = 3		
	Mean	SE	Rank	Mean	SE	Rank	Mean	SE	Rank	Mean	SE	Rank
Species Selected for Chemical Analysis												
Acacia nilotica	4.06±	3.34	9	1.77±	1.69	12	0.47±	0.47	21	-	-	-
Acacia tortilis	0.39±	0.36	25	0.05±	0.05	30	-	-	-	-	-	-
Burkea africana	11.93±	5.91	3	0.97±	0.48	15	0.48±	0.54	19	-	-	-
Combretum molle	1.10±	1.08	15	2.09±	1.06	9	7.16±	4.60	5	-	-	-
Dichrostachys cinerea	6.58±	3.33	6	5.75±	2.01	5	1.75±	0.98	11	-	-	-
Dombeya rotundifolia	5.75±	2.91	7	0.83±	0.39	17	9.34±	4.47	4	1.41±	0.91	9
Euclea natalensis	20.01±	9.55	1	4.25±	1.33	9	26.26±	13.20	1	64.71±	2.66	1
Grewia flavescens	12.13±	8.37	2	44.59±	14.96	1	20.14±	14.14	2	3.94±	2.08	4
Ochna pulchra	10.05±	8.07	4	4.45±	1.70	6	1.55±	1.14	12	0.16±	0.11	17
Peltophorum africanum	0.22±	0.22	28	0.07±	0.07	28	0.17±	0.17	27.5	-	-	-
Rhus leptodictya	0.39±	0.16	26	1.90±	1.22	10	10.26±	5.27	3	0.57±	2.28	14
Strychnos pungens	1.22±	0.65	13	1.78±	1.18	11	4.26±	1.97	6	1.95±	0.64	5
Terminalia sericea	-	-	-	0.61±	0.61	21	0.42±	0.31	23	-	-	-
Vitex rehmannii	1.14±	1.14	14	7.38±	7.72	2	2.99±	2.99	8	0.20±	0.12	16
Other Species												
Acacia burkei	0.86±	0.86	20.5	0.05±	0.05	30	-	-	-	-	-	-
Acacia caffra	-	-	-	-	-	-	-	-	-	-	-	-
Acacia hebeclada	-	-	-	-	-	-	-	-	-	-	-	-
Acacia karoo	-	-	-	0.11±	0.11	27	0.77±	0.72	15	-	-	-
Barleria bremekampii	-	-	-	-	-	-	-	-	-	-	-	-
Bequartiodendron magalismontanum	-	-	-	-	-	-	-	-	-	0.93±	0.93	11
Bridelia mollis	0.11±	0.11	33.5	0.40±	0.40	23	-	-	-	-	-	-
Canthium gilfillanii	0.15±	0.14	29	-	-	-	-	-	-	-	-	-
Carissa bispinosa	4.93±	4.30	8	0.84±	0.84	16	0.70±	0.56	17	6.49±	1.51	3
Cassine transvaalensis	0.03±	0.04	33.5	-	-	-	0.13±	0.05	29	0.02±	0.02	20.5
Combretum apiculatum	-	-	-	0.71±	0.71	19.5	1.35±	1.35	13	-	-	-

Table 4.3. Continued

Combretum zeyheri	-	-	-	0.16±	0.11	25	0.51±	0.29	20	1.40±	1.23	10
Croton gratissimus	-	-	-	-	-	-	-	-	-	-	-	-
Dichapetalum cymosum	-	-	-	-	-	-	-	-	-	-	-	-
Diospyros lycioides	0.58±	0.37	22.5	0.16±	0.11	25	0.51±	0.29	20	1.40±	1.23	10
Ehretia rigida	0.71±	0.54	18	0.72±	0.72	19.5	-	-	-	0.22±	0.22	15
Erythrococca menyharthii	0.47±	0.35	24	-	-	-	0.45±	0.24	22	0.09±	0.09	18
Euclea crispa	-	-	-	0 49±	0.49	22	0.02±	0.02	32	1.56±	1.56	8
Euclea undulata	2.36±	1.70	10	1.02±	1.02	6	2.50±	1.58	9	11.00±	2.75	2
Grewia bicolor	0.67±	0.39	19	-	-	-	0.85±	0.37	14	0.02±	0.02	20.5
Grewia flava	0.98±	0.86	16	0.75±	0.29	18	0.17±	0.09	27.5	0.06±	0.06	19
Grewia monticola	1.37±	0.23	12	0.04±	0.04	31	3.89±	1.44	7	0.60±	0.30	13
Lannea discolor	6.44±	6.44	5	6.03±	2.93	4	-	-	-	-	-	-
Lannea edulis	-	-	-	-	-	-	-	-	-	-	-	-
Maytenus tenuispina	0.58±	0.58	22.5	0.34±	0.34	24	-	-	-	-	-	-
Mundulea sericea	0.86±	0.53	20.5	-	-	-	-	-	-	-	-	-
Ozoroa paniculosa	0.92±	0.73	17	2.37±	2.34	8	0.35±	0.20	25	1.80±	0.86	6
Pappea capensis	-	-	-	-	-	-	0.04±	0.04	31	-	-	-
Protea welwitschii	-	-	-	-	-	-	-	-	-	-	-	-
Pseudolachnostylis *maprounifolia*	-	-	-	-	-	-	-	-	-	-	-	-
Pygmaeothamnus zeyheri	-	-	-	-	-	-	-	-	-	-	-	-
Rhus pyroides	0.09±	0.08	33.5	7.22±	6.26	3	0.22±	0.22	26	0.70±	0.17	12
Sclerocarya caffra	-	-	-	-	-	-	-	-	-	-	-	-
Securidaca longipedunculata	0.11±	0.11	31.5	0.15±	0.09	26	1.76±	1.30	10	-	-	-
Securinega virosa	-	-	-	-	-	-	-	-	-	-	-	-
Strychnos cocculoides	0.28±	0.15	27	1.60±	1.00	13	0.74±	0.74	16	-	-	-
Strychnos madagascariensis	-	-	-	-	-	-	-		-	-	-	-
Tarchonanthus camphoratus	-	-	-	-	-	-	0.63±	0.63	10	-	-	-
Vitex mombassae	-	-	-	-	-	-	-	-	-	-	-	-
Vangueria infaustra	-	-	-	-	-	-	0.06±	0.04	30	-	-	-
Ximenia caffra	1.72±	0.98	11	-	-	-	-	-	-	1.03±	1.35	7
Ziziphus mucronata	0.12±	0.12	30	-	-	-	-	-	-	0.17±	0.17	18

(Standard error calculated on a monthly basis in order to give equal weighting to each month) occurred in January 1982 following defoliation by caterpillars. These new leaves were also sought out by the kudus whilst mature green leaves on the same plant were ignored.

A common woody plant not seen to be eaten by the kudus was P. africanum. Many other less common species were only eaten infrequently.

ii. Impalas

Throughout the growing season the two woody plants forming the greatest proportion in the diet of the impalas were G. flavescens and D. cinerea. Together these species occupied 10% of the total feeding time and accounted for half the woody browse eaten (Table 4.3.ii.). Acacia species accounted for 13% of the browsing time, and C. molle for 3 to 4%. None of the evergreen species was eaten much in the growing season.

Those species favoured in the growing season continued to be eaten into the early dry season, and the use of V.rehmannii and Euclea undulata increased. The evergreen species, E. undulata dominated the diet in the late dry season at 30% of the browsing time. The use of other evergreens especially E. natalensis, S. pungens and Carissa bispinosa increased significantly from that of the early dry season. The dried leaves of C. molle, C. zeyheri, G. flavescens and T. sericea were also eaten in the late dry season.

Leaves of O. pulchra were only eaten in September, October and

January when newly flushed leaves were available, L. discolor was also only utilised when in new leaf in November and December. At no time did the impalas make much use of B. africana leaves.

iii. Goats

In the early growing season the goats ate many species of woody plants, including E. natalensis in the first month, but the main foods were G. flavescens and the new leaves of O. pulchra and B. africana (Table 4.3.iii.). The leaves of the latter two species, and those of L. discolor, were not eaten once they had hardened.

G. flavescens occupied about one third of the feeding time in the late growing season, significantly more than any other plant species. Other species frequently eaten at this season were V. rehmannii, Rhus pyroides and D. cinerea. Also eaten were the second flush of new O. pulchra leaves.

In the early dry season G. flavescens was still a principal food plant but less than in the growing season. R. leptodictya, C. molle and D. rotundifolia were also favoured in this season. The evergreen E. natalensis was eaten increasingly throughout the dry season until in the late dry season it was the major plant species in the diet, occupying a quarter of the total feeding time, or 65% of the browsing time. The use of E. natalensis continued in to the early part of the growing season before the deciduous species had fully leafed out. Other evergreens such as E. undulata, and Carissa bispinosa, together with the dead leaves of G. flavescens, comprised most of the other woody browse eaten during the late dry season.

iv. Comparison between the Animal Species

The relative dietary use of woody species was estimated from the proportion of the browsing time the animals spent eating each species, otherwise all comparisons were swamped by the the effects of the differential use of grass by the animals.

The proportions of the most common woody plant species in the diets of kudus and impalas were significantly correlated in the early growing season whilst the goats differed by their greater use of E. natalensis and O. pulchra (Fig 4.2.). By the late growing season the proportions of these species were significantly correlated for all the animals.

Throughout the growing and early dry seasons G. flavescens was highly favoured by all the animals. The impalas and kudus also ate the dead leaves of this species remaining on the bushes in the late dry season. The goats had a slightly, but not significantly, lower utilisation of this species in the early growing season.

Another generally favoured plant was D. cinerea. This species was eaten by all the animals in the growing season. The kudus and impalas in particular favoured this species and continued to use it well in to the early dry season.

The kudus and goats utilised V. rehmannii in the growing season rather more than the impalas did. These two animal species also showed a high utilisation of B. africana and O. pulchra in the early growing season. The impalas preferred to graze at this time of year. The kudus continued to feed on a second flush of O. pulchra leaves in the late growing season, and fed avidly on the new foliage of this species when it emerged in September.

The kudus were the only species to eat C. zeyheri, and to a lesser extent Ziziphus mucronata, in the early growing season. The goats preferred D. rotundifolia and L. discolor, and in the late growing season, R. pyroides. The impalas fed on Erythrococca menyharthii and three Acacia species significantly more than the goats and kudus did in the early growing season. The impalas also ate significantly more A. nilotica and A. tortilis than the kudus in the late growing season.

The species selection displayed in the early dry season was similar to that of the late growing season, but with the increased utilisation of evergreen species becoming evident. The proportions of the common woody species in the diets of the three animal species were no longer correlated due to the greater use of A. nilotica by the impalas and E. natalensis by the goats.

In the late dry season the kudus and impalas both ate much of the evergreen S. pungens. The dietary proportions of the two animal species were significantly correlated, the goats differed mainly by their high use of E. natalensis. Species used in common

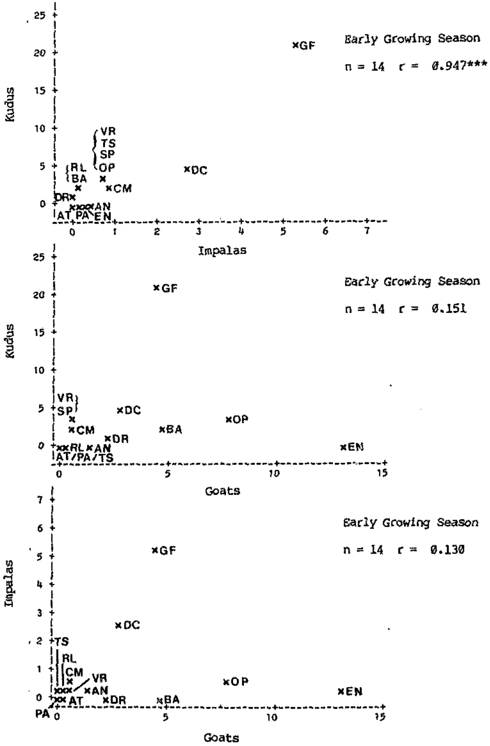


Fig 4.2. A Comparison of the Proportions of Woody Plant Species in the Diets of Kudus, Impalas and Goats.

i. Early Growing Season.

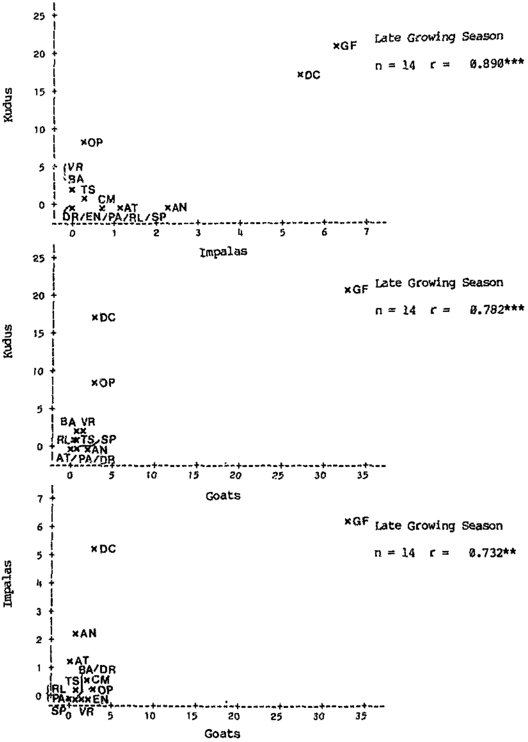


Fig 4.2. A Comparison of the Proportions of Woody Plant Species in the Diets of Kudus, Impalas and Goats.

ii. Late Growing Season.

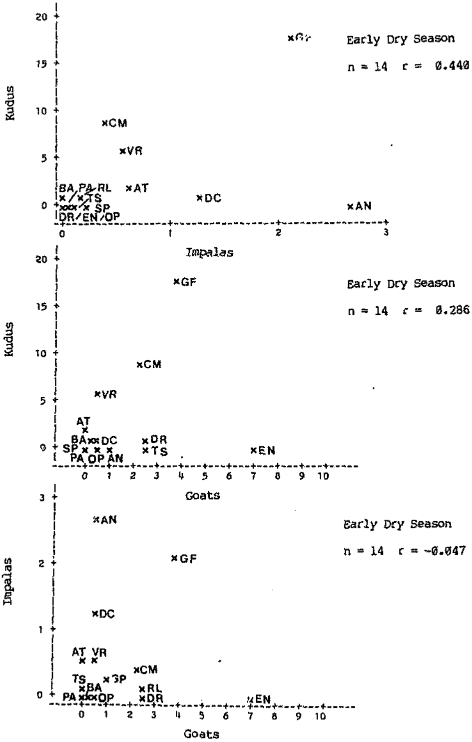


Fig 4.2. A Comparison of the Proportions of Woody Plant Species in the Diets of Kudus, Impalas and Goats.

iii. Early Dry Season.

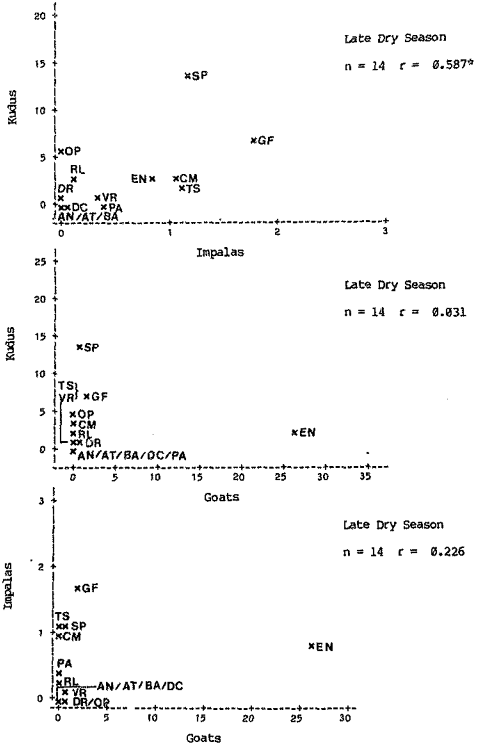


Fig 4.2. A Comparison of the Proportions of Woody Plant Species in the Diets of Kudus, Impalas and Goats.

iv. Late Dry Season.

by the impalas and goats were C. molle and the evergreens E. undulata, and C. bispinosa. All the animals showed an increase in the use of E. natalensis in the late dry season, but the proportion of this species in the diet of the goats far exceeded its use by the kudus and impalas. The goats, unlike the other animals, continued to eat this species well into the growing season. The kudus differed significantly in their use of D. lycioides and C. zeyheri in the dry season; they also made extensive use of the newly flushed leaves of D. lycioides in September when little other green browse was available. The impalas alone ate much T. sericea, but this species was eaten extensively as leaf-litter by both the impalas and goats.

b. Leaf-litter

Fallen leaves of three tree species, S. cocculoides, T. sericea and Z. mucronata, accounted for half the leaf-litter eaten by the goats in the dry season, and 80% of that eaten by the impalas. The kudus ate little leaf-litter but 60% of that eaten was from S. cocculoides trees. The kudus also ate the big leaves of C. zeyheri which were not favoured by the impalas and goats.

Besides the three dominant species the impalas favoured D. cinerea, S. pungens and A. tortilis litter in the early dry season and Strychnos madagascariensis litter in the late dry season (Table 4.4.). The goats ate significantly less S. cocculoides litter in the late dry season than in the previous season, having

Table 4.4. The Proportion of the Total Feeding Time (%) Spent Feeding on Leaf Litter.

i. Kudus

Species	Early Growing Season n = 19			Late Growing Season n = 19			Early Dry Season n = 14			Late Dry Season n = 17		
	Mean	SE	Rank	Mean	SE	Rank	Mean	SE	Rank	Mean	SE	Rank
Acacia burkei	-	-	-	-	-	-	-	-	-	-	-	-
Acacia caffra	-	-	-	-	-	-	-	-	-	0.12±	0.12	6
Acacia nilotica	-	-	-	-	-	-	-	-	-	-	-	-
Acacia tortilis	-	-	-	-	-	-	-	-	-	-	-	-
Burkea africana	-	-	-	-	-	-	-	-	-	-	-	-
Combretum apiculatum	-	-	-	-	-	-	-	-	-	-	-	-
Combretum molle	-	-	-	-	-	-	-	-	-	0.34±	0.20	3.5
Combretum zeyheri	-	-	-	-	-	-	-	-	-	1.54±	0.57	2
Dichrostachys cinerea	-	-	-	-	-	-	-	-	-	0.34±	0.20	3.5
Dombeya rotundifolia	-	-	-	-	-	-	-	-	-	-	-	-
Euclea natalensis	-	-	-	-	-	-	-	-	-	-	-	-
Euclea undulata	-	-	-	-	-	-	-	-	-	-	-	-
Grewia flavescens	-	-	-	-	-	-	-	-	-	-	-	-
Grewia monticola	-	-	-	-	-	-	-	-	-	-	-	-
Lannea discolor	-	-	-	-	-	-	-	-	-	-	-	-
Ozoroa paniculosa	-	-	-	-	-	-	-	-	-	-	-	-
Rhus leptodictya	0.03±	0.03	1	-	-	-	-	-	-	-	-	-
Sclerocarya caffra	-	-	-	-	-	-	-	-	-	-	-	-
Strychnos cocculoides	-	-	-	-	-	-	-	-	-	4.69±	2.52	1
Strychnos madagascariensis	-	-	-	-	-	-	-	-	-	-	-	-
Strychnos pungens	-	-	-	-	-	-	-	-	-	-	-	-
Terminalia sericea	-	-	-	-	-	-	-	-	-	0.28±	0.18	5
Vitex *rehmannii*	-	-	-	-	-	-	-	-	-	-	-	-
Ximenia caffra	-	-	-	-	-	-	-	-	-	-	-	-
Ziziphus mucronata	-	-	-	-	-	-	-	-	-	0.11±	0.11	7
Unidentified	-	-	-	-	-	-	-	-	-	-	-	-
Maize leaves	-	-	-	-	-	-	-	-	-	-	-	-

Table 4.4. *The Proportion of the Total Feeding Time (%) Spent Feeding on Leaf Litter.*

ii. Impalas

Species	Early Growing Season n = 23			Late Growing Season n = 30			*Early Dry* Season n = 34			Late Dry Season n = 32		
	Mean	SE	Rank	Mean	SE	Rank	Mean	SE	Rank	Mean	SE	Rank
Acacia burkei	-	-	-	0.02±	0.02	1	-	-	-	-	-	-
Acacia caffra	-	-	-	-	-	-	-	-	-	-	-	-
Acacia nilotica	-	-	-	-	-	-	0.09±	0.09	7	0.64±	0.34	8
Acacia tortilis	-	-	-	-	-	-	0.71±	0.59	3	0.39±	0.24	7
Burkea africana	-	-	-	-	-	-	-	-	-	-	-	-
Combretum apiculatum	-	-	-	-	-	-	0.23±	0.12	5	0.24±	0.17	9
Combretum molle	-	-	-	-	-	-	-	-	-	0.06±	0.04	11
Combretum zeyheri	-	-	-	-	-	-	-	-	-	0.05±	0.05	12
Dichrostachys cinerea	-	-	-	-	-	-	0.23±	0.12	5.5	1.02±	0.58	4
Dombeya rotundifolia	-	-	-	-	-	-	-	-	-	-	-	-
Euclea *natalensis*	-	-	-	-	-	-	-	-	-	-	-	-
Euclea undulata	-	-	-	-	-	-	-	-	-	-	-	-
Grewia flavescens	-	-	-	-	-	-	-	-	-	-	-	-
Grewia monticola	-	-	-	-	-	-	-	-	-	-	-	-
Lannea discolor	-	-	-	-	-	-	-	-	-	-	-	-
Ozoroa paniculosa	-	-	-	-	-	-	-	-	-	-	-	-
Rhus leptodictya	-	-	-	-	-	-	-	-	-	-	-	-
Sclerocarya caffra	-	-	-	-	-	-	0.01±	0.01	8.5	-	-	-
Strychnos cocculoides	0.01±	0.01	2	-	-	-	7.06±	2.96	1	12.23±	3.34	1
Strychnos madagascariensis	-	-	-	-	-	-	-	-	-	0.78±	0.75	5
Strychnos pungens	-	-	-	-	-	-	-	-	-	-	-	-
Terminalia sericea	0.31±	0.20	1	0.01±	0.01	2.5	0.40±	0.23	4	8.20±	2.71	2
Vitex rehmannii	-	-	-	-	-	-	-	-	-	-	-	-
Ximenia caffra	-	-	-	-	-	-	-	-	-	-	-	-
Ziziphus mucronata	-	-	-	-	-	-	1.50±	0.86	2	7.65±	2.76	3
Unidentified	-	-	-	0.01±	0.01	2.5	0.01±	0.01	8.5	0.11±	0.07	10
Maize leaves	-	-	-	-	-	-	-	-	-	0.28±	0.14	8

Table 4.4. The Proportion of the Total Feeding Time (%) Spent Feeding on Leaf Litter.

iii. Goats

Species	Early Growing Season n = 19			Late Growing Season n = 19			Early Dry Season n = 14			Late Dry Season n = 17		
	Mean	SE	Rank	Mean	SE	Rank	Mean	SE	Rank	Mean	SE	Rank
Acacia burkei	-	-	-	-	-	-	-	-	-	-	-	-
Acacia caffra	-	-	-	-	-	-	-	-	-	0.12±	0.12	6
Acacia nilotica	-	-	-	-	-	-	-	-	-	-	-	-
Acacia tortilis	-	-	-	-	-	-	-	-	-	-	-	-
Burkea africana	0.12±	0.08	9	-	-	-	-	-	-	-	-	-
Combretum apiculatum	-	-	-	-	-	-	0.06±	0.06	10	-	-	-
Combretum molle	0.13±	0.13	7.5	-	-	-	0.70±	0.54	5	0.09±	0.06	13
Combretum zeyheri	0.02±	0.02	11.5	-	-	-	0.16±	[illegible]	9	0.71±	0.38	7
Dichrostachys cinerea	-	-	-	-	-	-	0.38±	[illegible]	7	-	-	-
Dombeya rotundifolia	0.02±	0.02	11.5	-	-	-	-	-	-	0.29±	0.15	8.
Euclea natalensis	1.23±	0.72	1	-	-	-	-	-	-	1.24±	0.40	3
Euclea undulata	0.36±	0.36	4	-	-	-	-	-	-	-	-	-
Grewia flavescens	-	-	-	-	-	-	0.03±	0.03	11	-	-	-
Grewia monticola	-	-	-	-	-	-	-	-	-	0.05±	0.05	14
Lannea discolor	0.04±	0.03	10	-	-	-	-	-	-	-	-	-
Ozoroa paniculosa	-	-	-	-	-	-	-	-	-	0.13±	0.08	12
Rhus leptodictya	-	-	-	-	-	-	-	-	-	-	-	-
Sclerocarya caffra	0.13±	0.13	7.5	-	-	-	3.38±	1.98	4	-	-	-
Strychnos cocculoides	-	-	-	1.16±	1.16	3	22.90±	4.39	1	0.82±	0.33	5
Strychnos madagascariensis	-	-	-	-	-	-	-	-	-	-	-	-
Strychnos pungens	0.16±	0.16	6	-	-	-	-	-	-	0.13±	0.09	12.5
Terminalia sericea	0.18±	0.17	[illegible]	2.17±	1.92	1	9.03±	2.74	3	17.2[illegible]±	3.47	1
Vitex rehmannii	-	-	-	-	-	-	-	-	-	0.14±	0.14	10
Ximenia caffra	-	-	-	-	-	-	-	-	-	0.15±	0.14	9
Ziziphus mucronata	-	-	-	-	-	-	9.63±	3.18	2	5.29±	3.54	2
Unidentified	0.96±	0.44	3	1.70±	1.64	[illegible]	0.56±	0.26	6	0.92±	0.55	4
Maize leaves	0.58±	0.22	2	-	-	-	0.29±	0.13	4	0.79±	0.17	5

used up most of the fallen leaves available within their home range. In the late dry season the use of the ubiquitous T. sericea litter increased significantly. The goats ate a significantly greater proportion of T. sericea litter than either the impalas or kudus. The goats also began to eat some E. natalensis litter in the late dry season and continued to do so until December when plenty of green foliage was available. The kudus and impalas did not take E. natalensis litter.

None of the animals ate much B. africana litter and no O. pulchra litter was seen to be eaten even though the fallen leaves of this species formed thick carpets under the plants.

c. Forbs

Fo bs formed only a small part of the diet of the animals used in this study. There was a great diversity of forb species within the study area. Approximatly 350 species were recorded in the enclosure for the tame animals, and there was much variation in abundance of species between the two years of the study. The kudus were seen to eat 46% of the species they en ntered, the goats ate 39% and the impalas ate 27%. Consequently individual species occupied only a very small proportion of the total feeding time. For this reason only major differences in the feeding preferences of the animals can be proven statistically.

Table 4.5. The Proportion of the Time Spent Feeding on Forbs (%) Occupied by Individual Forb Species.

i. *Kudus*

Species	Early Growing Season n = 3			Late Growing Season n = 3			Early Dry Season n = 3			Late Dry Season n = 3		
	Mean	SE	Rank	Mean	SE	Rank	Mean	SE	Rank	Mean	SE	Rank
Species Selected [illegible]tical Analysis												
Evolvulus alsinoides	–	–	–	–	–	–	–	–	–	–	–	–
Hermannia grisea	2.72±	0.35	10	5.74±	1.85	8	4.26±	2.14	6	5.70±	0.57	6
Indigofera macra	0.54±	0.54	24	–	+ –	–	–	–	–	–	–	–
Justicia flava	0.87±	0.57	20	20.96±	7.88	1	12.80±	[illegible].76	3	0.98±	0.96	9
Oldenlandia herbacea	–	–	–	–	–	–	–	–	–	–	–	–
Pollichia campestris	11.89±	2.71	3	6.93±	1.89	7	6.10±	3.54	5	0.37±	0.37	13
Sida cordifolia	0.82±	0.18	21	7.42±	6.30	6	19.[illegible]	5.0	2	22.23±	11.96	2
Solanum panduraeforme	0.39±	0.22	30	–	–	–	–	–	–	2.90±	2.90	8
Tephrosia forbesii	–	–	–	–	–	–	0.54±	0.54	17	–	–	–
Waltheria indica	2.05±	1.70	14	8.59±	2.96	3	35.22±	18.04	1	30.90±	23.45	1
Other Species												
Achyropsis leptostachya	0.13±	0.13	44.5	–	–	–	–	–	–	0.15±	0.15	16
Agathisanthemum bojeri	–	–	–	1.71±	1.34	14	–	–	–	–	–	–
Aloe davyana	0.36±	0.20	31	–	–	–	–	–	–	–	–	–
Asparagus buchananii	2.89±	2.75	9	–	–	–	–	–	–	–	–	–
Asparagus suaveolens	1.23±	0.86	16	–	–	–	0.11±	0.11	20.5	–	–	–
Bauhinia macrantha	4.49±	2.25	6	–	–	–	–	–	–	–	–	–
Becium angustif[illegible]um	0.07±	0.07	49.5	–	–	–	0.20±	0.20	21	–	–	–
Blepharis maderaspatensis	0.42±	0.42	28.5	0.55±	0.30	21	–	–	–	–	–	–
Boophane disticha	0.12±	0.12	47.5	–	–	–	–	–	–	–	–	–
Cassia capensis	7.99±	3.97	4	7.49±	0.53	5	1.08±	0.89	11	–	–	–
Chaetacanthus costatus	13.31±	4.64	2	0.70±	0.70	20	2.09±	1.21	8	–	–	–
Commelina africana	3.95±	3.04	7	2.47±	0.05	12	0.58±	0.58	14.5	–	–	–
Commelina eckloniana	–	–	–	0.06±	0.06	29	–	–	–	–	–	–
Commelina erecta	0.05±	0.05	53.5	0.10±	0.10	27	–	–	–	–	–	–
Crabbea hirsuta	–	–	–	0.36±	0.36	24	–	–	–	–	–	–
Elephantorrhiza obliqua	14.09±	9.81	1	0.91±	0.91	18	0.41±	0.41	18.5	–	–	–
Fadogia monticola	0.52±	0.26	52	–	–	–	–	–	–	–	–	–
Felicia fascicularis	0.19±	0.09	43	0.13±	0.13	26	–	–	–	–	–	–
Gladeolus cf. calcartus	0.13±	0.13	44.5	–	–	–	–	–	–	–	–	–

Table 4.5 Continued. . .

Hemizygia petrensis	0.28±	0.28	36	-	-	-	-	-	-	-	-	-
Hermannia boraginiflora	0.06±	0.06	51.5	-	-	-	-	-	-	-	-	-
Hermbstaedtia odorata	1.01±	0.38	17	0.78±	0.78	19	-	-	-	-	-	-
Hypoxis obtusa	1.79±	0.48	15	-	-	-	-	-	-	-	-	-
Indigofera comosa	0.34±	0.24	33	2.55±	2.55	11	-	-	-	-	-	-
Indigofera nebrowniana	-	-	-	-	-	-	0.41±	0.41	18.5	-	-	-
Indigofera vicioides	0.24±	0.24	38.5	-	-	-	-	-	-	-	-	-
Ipomea obscura	0.31±	0.31	34.5	-	-	-	-	-	-	-	-	-
Justicia anagalloides	2.47±	1.24	12	0.17±	0.16	25	-	-	-	-	-	-
Justicia incerta	2.17±	1.63	13	3.21±	2.61	9	0.72±	0.61	12	-	-	-
Justicia minima	3.89±	0.55	8	8.40±	4.56	4	7.15±	4.46	4	9.83±	7.59	4
Justicia spergulaefolia	0.91±	0.56	18	1.05±	0.53	-	-	-	-	-	-	-
Lantana rugosa	0.06±	0.06	51.5	0.42±	0.42	23	-	-	-	-	-	-
Lippea javanica	0.26±	0.17	37	1.94±	0.21	13	3.41±	2.57	7	11.54±	10.10	3
Merremia tridentata	0.24±	0.24	38.5	-	-	-	-	-	-	-	-	-
Opuntia ficus-indica	-	-	-	-	-	-	-	-	-	0.38±	0.38	12
Pavonia transvaalensis	0.68±	0.68	23	2.75±	2.57	10	0.31±	0.31	20	-	-	-
Plumbago zeylanica	-	-	-	9.92±	9.81	2	-	-	-	-	-	-
Raphionacme burkei	0.07±	0.07	49.5	-	-	-	-	-	-	-	-	-
Rhynchosia longiflora	0.23±	0.23	40	-	-	-	0.58±	0.58	14.5	-	-	-
Ruellia cordata	0.76±	0.76	22	-	-	-	-	-	-	-	-	-
Salicia rehmannii	0.45±	0.45	26.5	0.51±	0.51	22	-	-	-	-	-	-
Schkuhria pinnata	2.67±	2.12	11	-	-	-	-	-	-	-	-	-
Senecio inaequidens	0.31±	0.21	34.5	-	-	-	-	-	-	-	-	-
Senecio venosus	0.80±	0.19	19	-	-	-	-	-	-	-	-	-
Sida alba	-	-	-	1.29±	0.93	16	-	-	-	-	-	-
Solanum coccineum	0.04±	0.04	55	1.82±	1.82	15	-	-	-	3.73±	3.73	6
Solanum seaforthianum	0.24±	0.24	38.5	-	-	-	-	-	-	-	-	-
Sphedamnocarpus pruriens	0.42±	0.42	28.5	-	-	-	-	-	-	9.73±	9.73	5
Sutera burkeana	0.22±	0.22	41	-	-	-	-	-	-	-	-	-
Tephrosia longipes	-	-	-	-	-	-	-	-	-	0.29±	0.29	14
Tephrosia lupinifolia	0.15±	0.15	44	-	-	-	-	-	-	-	-	-
Thunbergia neglecta	0.35±	0.35	32	-	-	-	0.55±	0.55	16	-	-	-
Triumfetta pentandra	0.12±	0.12	47.5	-	-	-	0.69±	0.50	13	-	-	-
Triumfetta sonderi	0.45±	0.45	26.5	-	-	-	-	-	-	0.61±	0.61	10
Vernonia oligocephala	6.72±	3.64	5	0.08±	0.08	28	0.15±	0.15	22	0.47±	0.47	11
Unidentified 1	0.05±	0.05	33.5	-	-	-	-	-	-	-	-	-
Unidentified 2	-	-	-	-	-	-	1.91±	1.91	9	-	-	-
Unidentified 3	-	-	-	-	-	-	1.37±	1.37	10	-	-	-

Table 4.5. The Proportion of the Time Spent Feeding on Forbs (%) Occupied by Individual Forb Species.

ii. Impalas

Species	Early Growing Season n = 3			Late Growing Season n = 3			Early Dry Season n = 3			Late Dry Season n = 3		
	Mean	SE	Rank	Mean	SE	Rank	Mean	SE	Rank	Mean	SE	Rank
Species selected for Chemical Analysis												
Evolvulus alsinoides	0.34±	0.34	29	0.90±	0.90	13	-	-	-	-	-	-
Hermannia grisea	2.32±	1.58	11	-	-	-	9.39±	6.13	2	3.73±	2.73	5
Indigofera macra	0.13±	0.13	36	1.30±	1.30	10	0.16±	0.10	20	-	-	-
Justicia flava	6.57±	6.17	4	-	-	-	-	-	-	1.95±	1.95	6
Oldenlandia herbacea	-	-	-	-	-	-	-	-	-	-	-	-
Pollichia campestris	5.70±	1.73	5	4.20±	3.68	4	7.97±	5.30	3	1.15±	1.15	7
Sida cordifolia	0.16±	0.16	34.5	0.14±	0.14	20.5	4.59±	2.49	5	7.55±	4.06	3
Solanum panduraeforme	4.05±	3.18	6	26.16±	10.70	2	3.76±	2.26	7	-	-	-
Tephrosia forbesii	1.48±	1.48	18	2.91±	1.50	5	6.07±	6.07	4	-	-	-
Waltheria indica	3.27±	1.39	9	36.62±	17.45	1	50.71±	21.22	1	44.73±	22.72	1
Other Species												
Acanthosicyos naudiniana	1.41±	1.41	19	-	-	-	-	-	-	-	-	-
Achyranthes sicula	1.89±	1.89	13.5	2.68±	2.68	6	3.09±	3.06	9	-	-	-
Agathisanthemum bojeri	-	-	-	-	-	-	0.10±	0.10	24	-	-	-
Asparagus buchananii	-	-	-	-	-	-	-	-	-	0.44±	0.44	9
Asparagus suaveolens	8.99±	4.60	3	0.43±	0.43	19	3.17±	2.00	8	1.70±	0.60	8
Becium angustifolium	1.80±	0.64	16	-	-	-	0.14±	0.14	21	-	-	-
Brayulinea densa	-	-	-	-	-	-	1.35±	1.35	10	-	-	-
Cassia capensis	1.04±	1.04	23	-	-	-	-	-	-	-	-	-
Chaetacanthus costatus	10.30±	9.20	2	-	-	-	-	-	-	-	-	-
Commelina africana	1.72±	1.28	17	0.14±	0.14	20.5	1.26±	1.13	11	-	-	-
Commelina erecta	1.06±	1.06	22	0.05±	0.05	22	0.09±	0.09	25.5	-	-	-
Crabbea hirsuta	-	-	-	-	-	-	4.04±	4.04	6		-	-
Dicerocaryum zanguebarium	-	-	-	-	-	-	1.23±	0.87	12	-	-	-
Elephantorrhiza obliqua	0.27±	0.27	30	-	-	-	-	-	-	-	-	-
Felicia fascicularis	1.84±	1.34	15	0.65±	0.65	16.5	-	-	-	-	-	-
Felicia muricata	-	-	-	0.65±	0.65	16.5	-	-	-	-	-	-

Table 4.5. Continued. . .

Gomphrena celosioides	0.20±	0.20	32	-	-	-	-	-	-	-	-	-
Hermannia boraginiflora	0.81±	0.81	25	-	-	-	-	-	-	-	-	-
Hermbstaedtia odorata	-	-	-	-	-	-	-	-	-	0.29±	0.29	10
Hibiscus meeusei	-	-	-	1.39±	1.39	9	-	-	-	-	-	-
Hibiscus subreniformis	-	-	-	0.04±	0.04	23.5	-	-	-	-	-	-
Indigofera daleoides	1.21±	1.21	21	-	-	-	0.24±	0.24	18	-	-	-
Ipomea *obscura*	1.89±	1.89	13.5	-	-	-	-	-	-	-	-	-
Jatropha zeyheri	0.07±	0.07	37	-	-	-	0.20±	0.20	19	-	-	-
Justicia incerta	4.66±	2.48	7	-	-	-	-	-	-	-	-	-
Justicia minima	23.06±	7.94	1	0.04±	0.04	23.5	-	-	-	4.88±	4.88	4
Justicia spergulaefolia	0.47±	0.47	27	-	-	-	-	-	-	-	-	-
Lantana rugosa	-	-	-	0.87±	0.87	14	0.11±	0.1	23	-	-	-
Lippea javanica	1.30±	0.90	20	0.02±	0.02	25	0.05±	0.05	27.5	33.93±	33.04	2
Merremia tridentata	-	-	-	2.69±	1.35	7	-	-	-	-	-	-
Pavonia transvaalensis	0.61±	0.61	26	-	-	-	-	-	-	-	-	-
Pentarrhinum insipidum	-	-	-	-	-	-	0.40±	0.40	16	-	-	-
Phyllanthus parvulus	1.01±	1.01	24	-	-	-	-	-	-	-	-	-
Plumbago zeylanica	2.96±	2.96	10	1.17±	0.85	11	0.61±	0.61	14	-	-	-
Polygala sphenoptera	-	-	-	1.74±	1.74	8	-	-	-	-	-	-
Portulaca quadrifida	0.20±	0.28	32	-	-	-	0.28±	0.28	17	-	-	-
Pterococcus africana	-	-	-	10.90±	10.82	3	0.64±	0.64	13	-	-	-
Rhynchosia venulosa	3.64±	3.64	8	0.60±	0.60	18	-	-	-	-	-	-
Sida chrysantha	0.16±	0.16	34.5	-	-	-	-	-	-	-	-	-
Solanum coccineum	2.04±	1.18	12	0.79±	0.59	15	-	-	-	-	-	-
Solanum incanum	0.20±	0.12	32	-	-	-	-	-	-	-	-	-
Trochomeria macrocarpa	-	-	-	0.94±	0.94	12	-	-	-	-	-	-
Vernonia oligocephala	0.35±	0.35	28	-	-	-	-	-	-	0.28±	0.28	11
Unidentified 1	-	-	-	-	-	-	0.05±	0.05	27.5	-	-	-
Unidentified 2	-	-	-	-	-	-	0.09±	0.09	25.5	-	-	-
Unidentified 3	-	-	-	-	-	-	0.53±	0.53	15	-	-	-

Table 4.5. *The Proportion of the Time Spent Feeding on Forbs (%) Occupied by Individual Forb Species.*

iii. Goats

Species	Early Growing Season n = 3			Late Growing Season n = 3			Early Dry Season n = 3			Late Dry Season n = 3		
	Mean	SE	Rank	Mean	SE	Rank	Mean	SE	Rank	Mean	SE	Rank
Species Selected for Chemical Analysis												
Evolvulus alsinoides	14.56±	14.56	3	3.05±	1.19	5	0.04±	0.04	17.5	–	–	–
Hermannia grisea	24.01±	11.66	1	1.30±	0.53	16	11.10±	6.63	2	23.63±	4.51	2
Indigofera macra	1.05±	1.05	13	3.05±	3.05	9	0.01±	0.01	24	–	–	–
Justicia flava	5.63±	2.82	5	–	–	–	3.02±	2.59	4	31.05±	13.65	1
Oldenlandia herbacea	0.15±	0.15	–	–	–	–	–	–	–	–	–	–
Pollichia campestris	19.54±	11.50	2	15.82±	3.96	3	2.68±	1.73	5	1.80±	0.84	6
Sida cordifolia	0.25±	0.25	25.5	0.05±	0.05	31.5	1.36±	1.29	6	17.96±	8.67	3
Solanum panduraeforme	0.25±	0.25	25.5	–	–	–	0.04±	0.04	17.5	0.03±	0.03	18
Tephrosia forbesii	–	–	–	27.63±	16.63	1	0.69±	0.44	9	–	–	–
Waltheria indica	4.99±	4.04	6	0.12±	0.12	28	68.12±	2.89	1	15.39±	7.25	4
Other Species												
Achyropsis leptostachya	1.64±	1.64	9	3.14±	3.14	7	–	–	–	4.43±	2.90	8
Achyranthes sicula	–	–	–	2.05±	1.04	12	7.98±	7.98	3	–	–	–
Asclepias burchellii	1.43±	1.43	12	–	–	–	–	–	–	–	–	–
Asclepias fruticosa	0.90±	0.90	14.5	0.88±	0.72	18	–	–	–	–	–	–
Asparagus buchananii	0.56±	0.38	20.5	–	–	–	–	–	–	–	–	–
Asparagus suaveolens	11.15±	4.76	4	0.73±	0.51	20	0.03±	0.03	20.5	0.23±	0.1[illegible]	15
Bauhinia macrantha	–	–	–	0.75±	0.75	19	–	–	–	–	–	–
Becium angustifolium	2.62±	1.73	7	2.52±	2.52	10	–	–	–	–	–	–
Blepharis maderaspatensis	–	–	–	–	–	–	1.66±	1.66	7	–	–	–
Borreria scabra	–	–	–	0.18±	0.18	26	–	–	–	–	–	–
Cassia capensis	–	–	–	3.45±	2.88	6	–	–	–	–	–	–
Cleome maculata	0.05±	0.05	30.5	0.06±	0.06	30	–	–	–	–	–	–
Commelina africana	2.43±	2.06	8	0.05±	0.05	31.5	–	–	–	0.20±	0.20	16
Commelina erecta	–	–	–	0.21±	0.21	24	–	–	–	–	–	–
Corchorus kirkii	–	–	–	–	–	–	–	–	–	0.55±	0.55	12
Crabbea hirsuta	–	–	–	–	–	–	0.59±	0.59	11	–	–	–

Table 4.5. Continued. . .

Dicoma macrocephala	-	-	-	-	-	-	0.03±	0.03	20.5	-	-	-
Felicia fascicularis	0.65±	0.58	10	-	-	-	0.03±	0.03	20.5	-	-	-
Felicia muricata	-	-	-	-	-	-	0.09±	0.09	15	-	-	-
Gladeolus cf. calcartus	-	-	-	0.54±	0.54	23	-	-	-	-	-	-
Hermbstaedtia odorata	0.56±	0.56	20.5	1.65±	1.37	14	-	-	-	-	-	-
Hypoxis obtusa	0.73±	0.74	17	-	-	-	-	-	-	-	-	-
Indigofera daleoides	-	-	-	1.07±	1.43	13	0.17±	0.17	13	0.15±	0.15	17
Ipomea obscura	0.21±	0.21	27	-	-	-	-	-	-	-	-	-
Justicia incerta	-	-	-	-	-	-	0.25±	0.14	12	0.69±	0.69	9
Justicia minima	-	-	-	-	-	-	0.05±	0.05	16	-	-	-
Kalanchoe paniculata	-	-	-	0.91±	0.53	17	-	-	-	-	-	-
Kohautia virgata	-	-	-	0.08±	0.08	29	-	-	-	-	-	-
Lantana rugosa	-	-	-	0.16±	0.16	27	-	-	-	-	-	-
Lippea javanica	-	-	-	-	-	-	-	-	-	0.64±	0.64	10.5
Melhania prostrata	0.08±	0.08	30	-	-	-	-	-	-	-	-	-
Merremia tridentata	-	-	-	15.92±	10.02	2	-	-	-	-	-	-
Pentarrhinum insipidum	0.60±	0.42	19	5.16±	1.00	4	-	-	-	-	-	-
Phyllanthus parvulus	1.50±	1.50	10	-	-	-	-	-	-	-	-	-
Portulaca quadrifida	0.90±	0.90	14.5	-	-	-	-	-	-	-	-	-
Pterococcus africana	-	-	-	2.30±	2.30	11	0.74±	0.49	8	-	-	-
Rhynchosia confusa	0.15±	0.15	28.5	1.62±	1.55	15	-	-	-	-	-	-
Rhynchosia longiflora	-	-	-	0.19±	0.19	25	-	-	-	-	-	-
Rhynchosia venulosa	-	-	-	0.59±	0.59	22	-	-	-	-	-	-
Senecio inaequidens	0.28±	0.28	24	2.79±	1.55	9	-	-	-	-	-	-
Sida alba	0.05±	0.05	30.5	-	-	-	-	-	-	-	-	-
Solanum coccineum	1.44±	1.09	11	-	-	-	0.67±	0.67	10	0.43±	0.43	13.5
Solanum incanum	0.34±	0.34	23	-	-	-	-	-	-	-	-	-
Sphedamnocarpus pruriens	-	-	-	-	-	-	-	-	-	0.72±	0.72	8
Talinum caffrum	0.86±	0.86	16	-	-	-	-	-	-	-	-	-
Triumfetta sonderi	-	-	-	-	-	-	0.03±	0.03	20.5	-	-	-
Vernonia oligocephala	-	-	-	0.61±	0.61	21	-	-	-	1.04±	1.04	7
Unidentified 1	-	-	-	-	-	-	0.11±	0.11	14	-	-	-
Unidentified 2	0.43±	0.43	22	-	-	-	-	-	-	0.43±	0.43	13.5

i. Kudus

The major forb species in the diet of the kudus in the early growing season were Pollichia campestris, Chaetacanthus costatus, and Elephantorrhiza obliqua, all of which occupied over 10% of the time spent feeding on forbs (Table 4.5.i.). Other important species were Cassia capensis and Vernonia oligocephala. In the late growing season the use of Justicia flava and Waltheria indica increased significantly. C. capensis, and P. campestris continued to be well eaten along with Justicia minima, Plumbago zeylar and Sida cordifolia. These species with the exception of C. capensis remained as the major forb species in the early dry season, with W. indica and S. cordifolia being the most utilised species. Together these two species accounted for half the time spent feeding on forbs. The use of P. campestris and J. flava decreased towards the end of the dry season, but otherwise the species eaten remained similar throughout the dry season, only the perennial forb Lippea javanica showed an increase in utilisation.

ii. Impalas

The forb species occupying the greatest proportion of the feeding time of the impalas in the early growing season were J. minima, Asparagus suaveolens, C. costatus, P. campestris and J. flava (Table 4.5.ii). P. campestris was also eaten in the late growing season along with Pavonia transvaalensis, W. indica, and S. panduraeforme. The latter two species accounting for 64% of the time the impalas spent eating forbs in this season. In the early dry season there was a significant increase in the use of W. indica until it became the dominant forb in the diet at 50% of the forb eating time. P. campestris continued to be well eaten along with H. grisea, and T. forbesii. In the late dry season W. indica remained as the most important food species along with L. javanica and to a lesser extent S. cordifolia.

iii. Goats

In the [illegible]ing season the forb species eaten most by the goats were [illegible]sea, P. campestris, A. suaveolens and Evolvulus alsinoides (Table 4.5.iii.). P. campestris continued to be eaten throughout the year until the late dry season when there was a significant decrease in utilisation as the plants dried out. T. forbesii formed 27% of the late growing season diet of forbs, significantly more than at any other time. M. tridentata was also eaten in this season. In the early dry season W. indica and H. grisea formed a significantly greater proportion of the feeding time than any other forb species up to 68% of the forb eating time being devoted to W. indica. The goats continued to utilise these two species throughout the late dry season together with S. cordifolia and the leafless green stalks of J. flava.

iv. Comparison between the Animal Species

The dietary proportions of forb species by the three animals generally did not correspond very closely, nor for the common species on a seasonal basis (Fig. 4.3.).

P. campestris was well eaten by all the animals when it was green. Justicia species also appeared to be generally favoured but were of patchy distribution and not always encountered by the animals.

In the early growing season C. costatus was favoured by the kudus and impalas but not encountered by the goats. Similarly E. obliqua and V. oligocephala, both favoured by the kudus, did not occur within the home range of the goats. The impalas did not favour these two species. The thorny forb A. suaveolens was utilised more by the impalas and goats than by the larger kudus. The goats alone had a high utilisation of H. grisea and E. alsinoides.

In the late growing season the animals differed in their use of many species, in particular much S. panduraeforme and W. indica was eaten by the impalas. The goats differed in their utilisation of T. forbesii and the kudus in eating much J.flava and several species not available to the goats.

P. campestris and especially W. indica were important as food plants to all the animals in the early dry season. At this time the species utilisation by impalas and goats was significantly correlated, but the kudus differred in their higher use of J. flava and S. cordifolia.

The diets of the kudus and impalas were significantly correlated in the late dry season when both species favoured the stemmy, perennial forbs, L. javanica, S. cordifolia and W. indica.

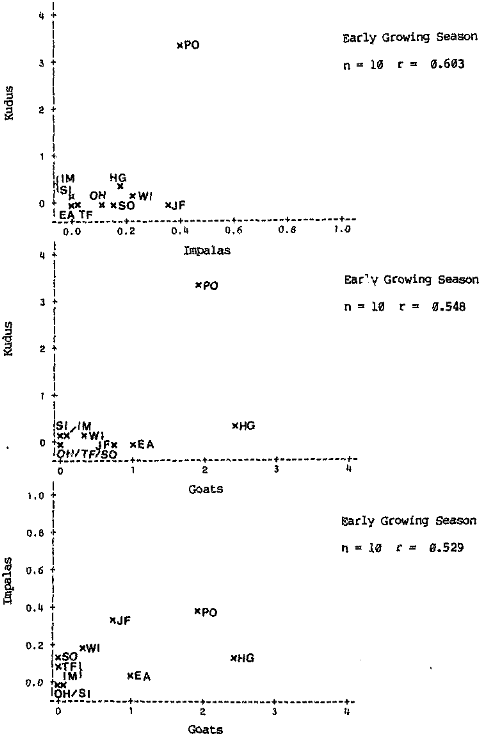


Fig 4.3. A Comparison of the Proportions of Forb Species in the Diets of Kudus, Impalas and Goats.

i. Early Growing Season.

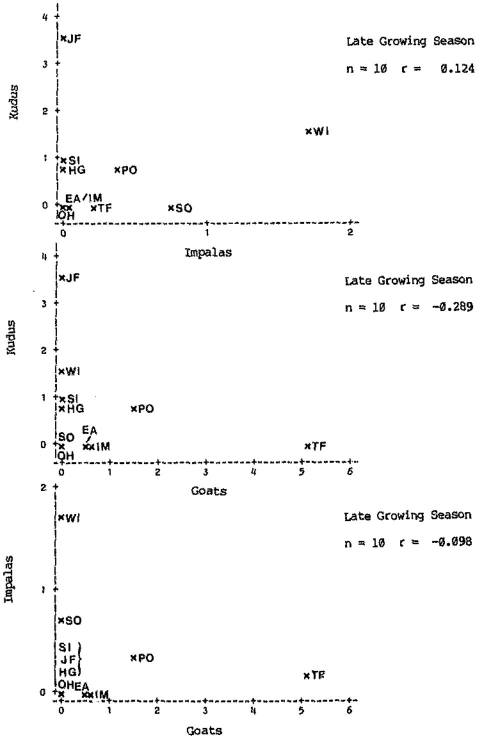


Fig 4.3. A Comparison of the Proportions of Forb Species in the Diets of Kudus, Impalas and Goats.

ii. Late Growing Season.

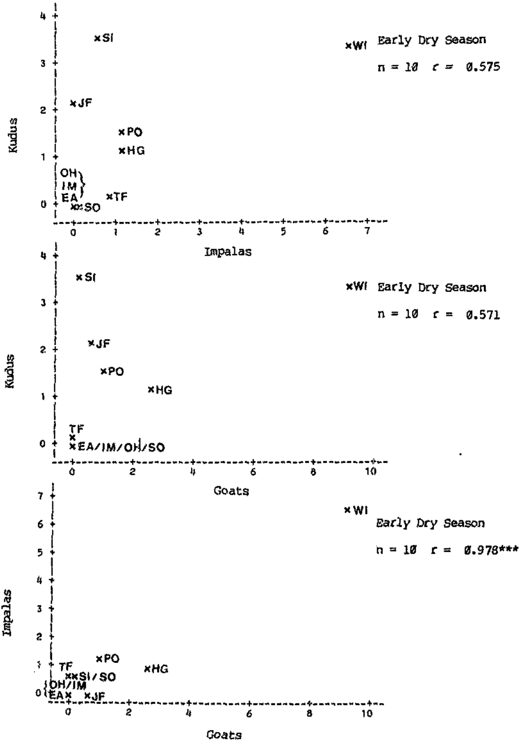


Fig 4.3. A Comparison of the Proportions of Forb Species in the Diets of Kudus, Impalas and Goats.

iii. Early Dry Season.

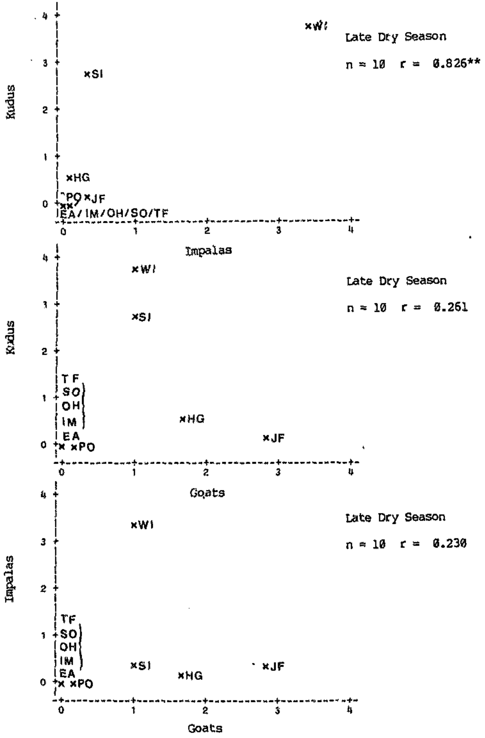


Fig 4.3. A Comparison of the Proportions of Forb Species in the Diets of Kudus, Impalas and Goats.

iv. Late Dry Season.

The goats used less of these species, instead they ate more J. flava and the perennial H. grisea.

4.4.3. Species Selection : *Selectivity Ratio*

The woody plant species with the most foliage below 2.5 m., and hence available to the large herbivores,was the shrub O. pulchra. This plant occurs in thickets and accounted for over half the available biomass of woody browse material in the enclosure at the peak of the growing season. The shrub G. flavescens and the dominant tree B. africana accounted *for a further* 25% of the available biomass, while trees of T. sericea, D. rotundifolia and two Acacia species, A. nilotica and A. tortilis, were also abundant.

a. *Similarities* between the Animal Species

When the relative quantities of each browse plant species eaten during the late growing season were compared with the available biomass of foliage of these species certain patterns of preference emerge. The plants were classified into three groups: selected species were of greater abundance in the diet relative to the environment, *non-selected species formed* a smaller proportion of the diet in relation to their abundance in the environment, while species occupying a similar proportion of the diet to their occurrence in the habitat were classified as intermediate. Fairly equal numbers of the rare woody plant species fell into the selected and non-selected categories (Fig 4.4.). Species preferred

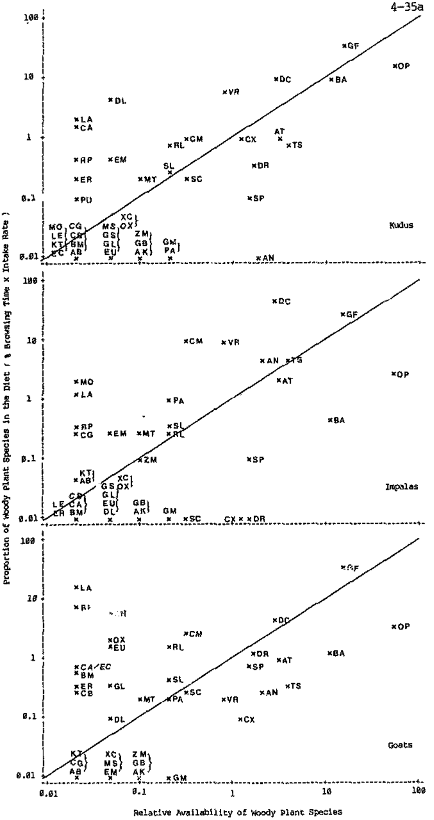


Fig 4.4. The Relative Abundance of Woody Plant Species in the Habitat Compared to the Proportion in the Diets of Browsing Ungulates in the Late Growing Season (Selectivity Ratio)

Plant Species Code:-

AB = Acacia burkei
AK = Acacia karoo
AN = Acacia nilotica
AT = Acacia tortilis
BM = Bridelia mollis
BA = Burkea africana
CG = Canthium gilfillanii
CB = Carissa bispinosa
KT = Cassine transvaalensis
CA = Combretum apiculatum
CM = Combretum molle
CX = Combretum zeyheri
DC = Dichrostachys cinerea
DL = Diospyros lycioides
DR = Dombeya rotundifolia
ER = Ehretia rigida
EM = Erythrococca menyharthii
EC = Euclea crispa
EN = Euclea natalensis
EU = Euclea undulata
GS = Gardenia spatulifolia
GB = Grewia bicolor
GL = Grewia flava
GF = Grewia flavescens
GM = Grewia monticola
LA = Lannea discolor
LE = Lannea edulis
MT = Maytenus tenuispina
MS = Mundulea sericea
OP = Ochna pulchra
OX = Ozoroa paniculosa
PC = Pappea capensis
PA = Peltophorum africanum
PU = Pseudolachnostylis maprounifolia
RL = Rhus leptodictya
RP = Rhus pyroides
MO = Sclerocarya caffra
SL = Securidaca longipedunculata
SC = Strychnos cocculoides
SP = Strychnos pungens
TS = Terminalia sericea
VR = Vitex rehmannii
XC = Ximenia caffra
ZM = Ziziphus mucronata

by all the ungulates were the Rhus species, two of the three Combretum species, Ehretia rigida, Erythrococca menyharthii and L. discolor. Species eaten in similar proportions to their availability were the abundant species, G. flavescens, and two less common species, Maytenus tenuispina and Securidaca longipedunculata. Neglected species included O. pulchra, the three less common Grewia species, Acacia karoo, Mundulea sericea and two evergreen species Gardenia spatulifolia and Ximenia caffra.

b. Differences between the Animal Species

The selectivity ratios of the common woody plant species for the three animal species were not significantly correlated (Fig 4.5.). This was mainly due to the apparent selection for E. natalensis by the goats. There are also differences in the selection of less common woody plant species.

i. Kudus

The kudus selected Pseudolachnostylis maprounifolia and Lannea edulis which were not encountered by the impalas and goats in the late growing season. B. africana and C. zeyheri were eaten in similar proportions as they were encountered by the kudus but were not eaten much by the impalas and goats.

ii. Impalas

The impalas ate a greater proportion of the common thorny Acacia species and *Z. mucronata* than did the kudus and goats for which these thorny species were non-selected. The impalas also had the strongest selection for the spiny plant *D. cinerea*. *T. sericea* was eaten most by the impalas, but *V. rehmanni*, a selected food plant of the kudus and goats was not favoured by the impalas. The impalas alone encountered *Cassine transvaalensis*, *Acacia burkei*, *S. caffra* and *Canthium gilfillanii*, all of which were favoured.

iii. Goats

The goats selected several evergreen species, including *S. pungens* and the three *Euclea* species. These were rarely, if at all, eaten by the kudus and impalas when deciduous plant were available.

4.3.4. Species Selection: Acceptance value

a. Behavioural Observations

The acceptance value of a plant species rarely reached 100%. This may be because the animals eat a wide variety of plant species and are possibly less likely to eat a plant if it is encountered soon after eating a plant of the same species. Whether or not a plant is eaten must also be influenced by the presence of neighbouring species of different palatability to the herbivore.

During a feeding bout the animals tend to feed on one level; for example when feeding in the herbaceous layer the animals may

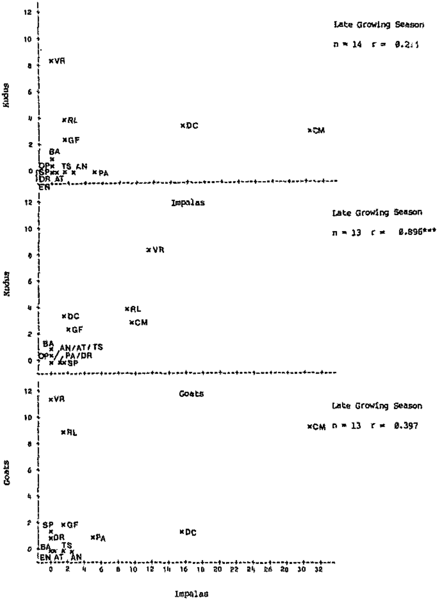


Fig 4.5. A Comparison of the Selectivity Ratios of Kudus, Impalas and Goats in the Late Growing Season.

ignore many woody plants in passing. This was particularly evident for the impalas which spent much time grazing. The acceptance value may also be influenced by the foraging patterns of the animals. Generally the goats scored higher acceptance values for many species than the kudus because they forage slowly over a small area. The kudus, in comparison, were more mobile so possibly missed plants which would have been eaten by an animal moving more slowly through the area. Consequentially it is not valid to compare the acceptance values for a plant species by different animal species numerically.

b. The Acceptance of the Common Woody Plants Species Selected for Chemical Analysis

i. Kudus

In the growing season the kudus had a high acceptance of G. flavescens, D. cinerea, and V. rehmannii (Table 4.6.i.). Species eaten only when in new leaf were O. pulchra, B. africana and D. rotundifolia. The acceptance of O. pulchra increased temporarily in January when a second flush of new leaves occurred following defoliation by caterpillars. The two Acacia species and C. molle were of moderate acceptance to kudus. P. africanum and the evergreen E. natalensis were of lowest acceptance. The other two evergreens S. pungens and R. leptodictya were of moderate acceptance in the early growing season but of low acceptance in the late growing season when food was most plentiful.

Table 4.6. Comparison between the Seasonal Acceptance Values of Common Woody Plants using the 2X2 Contingency Test.

i. kudus

	Early Growing Season Acceptance			Diff. EGS-LGS	Late Growing Season Acceptance			Diff. LGS-EDS	Early Dry Season Acceptance			Diff. EDS-LDS	Late Dry Season Acceptance			Diff. LDS-EWS
Species	%	n	class	Chi2	%	n	class	Chi2	%	n	class	Chi2	%	n	class	Chi2
Acacia nilotica	10	20	C	0.229	0	14	E	0.017	6	34	D	13.285***	71	7	A	7.240**
Acacia tortilis	–	0	–	–	33	12	B	0.000	28	29	B	0.001	17	6	C	–
Burkea africana	12	522	C	0.780	10	294	C	1.370	7	172	D	2.791	4	113	E	5,888*
Combretum molle	17	106	C	0,030	16	75	C	0.004	16	45	C	11.382***	47	64	A	17.232***
Dichrostachys cinerea	32	170	B	26.350***	42	213	A	1.179	36	160	B	0.002	43	7	A	2.311
Dombeya rotundifolia	11	126	C	2.220	5	93	D	1.858	1	102	E	12.839***	17	72	C	1.239
Euclea natalensis	2	95	E	0.463	0	91	E	3.067	5	73	D	10.281**	25	113	B	19.698***
Grewia flave s	37	514	B	0.253	35	533	B	0.681	32	394	B	0.187	31	240	B	2.379
Ochna p	5	1665	D	51.502***	13	902	C	43.240***	0	328	E	29.069***	10	478	C	13.449***
Peltop	0	16	E	0.000	0	25	E	0.000	0	28	E	0.000	0	6	E	0.000
Rhus le	18	17	C	0.985	9	22	D	0.937	24	25	B	3.207	55	11	A	2.648
Strychnos pu	17	151	C	9,948**	4	108	E	0.007	5	39	D	22.273***	48	172	A	33.511***
Terminalia sericea	5	154	D	3,192	11	74	C	1.457	4	72	E	34.671***	60	25	A	61.357***
Vitex rehmannii	44	90	A	0.001	43	30	A	10.874***	80	49	A	2.407	62	21	A	2.080

(Significance Levels : * P < 0.05; ** P < 0.01; *** P < 0.001)

Class A = Highly favoured	Acceptance = 40+
B = Favoured	= 20 – 40
C = Intermediate	= 10 – 20
D = Less favoured	= 5 – 10
E = Non-favoured	= 0 – 5

Table 4.6. Comparison between the Seasonal Acceptance Values of Common Woody Plants using the 2X2 Contingency Test.

ii. impalas

	Early Growing Season			Diff.	Late Growing Season			Diff.	Early Dry Season			Diff.	Late Dry Season			Diff.
	Acceptance			EGS-LGS	Acceptance			LGS-EDS	Acceptance			EDS-LDS	Acceptance			LDS-EWS
Species	%	n	class	Chi2	%	n	class	Chi2	%	n	class	Chi2	%	n	class	Chi2
Acacia nilotica	25	56	B	2.387	37	94	B	26.227***	6	79	D	0.024	0	11	E	2.128
Acacia tortilis	7	30	D	2.806	23	69	B	3.364	12	97	C	2.297	0	25	E	0.382
Burkea africana	4	136	E	1.030	1	113	E	0.014	0	89	E	0.000	0	56	E	0.912
Combretum molle	17	113	C	1.097	11	79	C	6.321*	31	36	B	0.114	27	55	B	2.506
Dichrostachys cinerea	28	192	B	1.435	23	259	B	5.809*	35	133	B	3.155	22	9	B	0.000
Dombeya rotundifolia	1	156	E	0.420	0	143	E	0.000	0	130	E	6.629*	8	37	D	3.148
Euclea natalensis	0	95	E	0.020	4	79	E	0.000	0	133	E	20.029***	20	143	B	20.004***
Grewia flavescens	22	455	B	2.8[illegible]	17	380	C	1.696	21	455	B	0.110	20	295	B	0.475
Ochna pulchra	7	415	E	3.261	4	322	E	13.074***	0	369	E	0.003	0	326	E	20.131***
Peltoporum africanum	6	[illegible]	D	1.152	1	76	E	0.150	2	47	E	0.473	9	22	D	0.002
Rhus leptodictya	21	29	B	0.213	13	31	C	3.359	45	11	A	0.000	57	3	-	1.103
Strychnos pungens	26	46	B	0.306	14	14	C	0.359	5	57	D	18.845***	36	170	b	1.733
Terminalia sericea	37	27	B	1.132	25	51	B	1.627	9	22	D	3.845*	50	8	A	0.060
Vitex rehmannii	16	19	C	0.017	12	17	C	0.232	22	32	B	3.316	50	12	A	2.682

(Significance Levels ; * P < 0.05; ** P < 0.01; *** P < 0.001)

Class A = Highly favoured — Acceptance = 40+
B = Favoured — = 20 - 40
C = Intermediate — = 10 - 20
D = Less favoured — = 5 - 10
E = Non-favoured — = 0 - 5

Table 4.6. Comparison between the Seasonal Acceptance Values of Common Woody Plants using the 2X2 Contingency Test.

iii. goats

	Early Growing Season			Diff.	Late Growing Season			Diff.	Early Dry Season			Diff.	Late Dry Season			Diff.
	Acceptance			EGS-LGS	Acceptance			LGS-EDS	Acceptance			EDS-LDS	Acceptance			LDS-EWS
Species	%	n	class	Chi2	%	n	class	Chi2	%	n	class	Chi2	%	n	class	Chi2
Acacia nilotica	73	15	A	3.762	[illegible]		-	3.003	9	32	D	0.022	0	8	E	8.497**
Acacia tortilis	80	5	A	0.320	33	3	B	0.024	0	4	-	0.000	0	1	-	0.150
Burkea africana	45	154	A	26.509***	4	51	E	0.108	3	61	E	0.054	0	14	E	8.873**
Combretum molle	8	49	D	13.293***	53	17	A	0.572	42	45	A	0.702	0	3	-	0.361
Dichrostachys cinerea	31	85	B	2.316	44	43	A	8.076**	8	25	D	-	-	0	-	-
Dombeya rotundifolia	36	104	B	5.564*	17	52	C	0.929	26	91	B	0.064	24	38	B	1.797
Euclea natalensis	62	145	A	22.856***	26	62	B	2.832	37	239	B	123.100***	84	282	A	26.806***
Grewia flavescens	16	317	C	56.842***	46	228	A	41.965***	21	353	B	2.886	27	188	B	8.358**
Ochna pulchra	51	366	A	50.113***	16	149	C	5.853*	8	204	D	1.047	4	100	E	66.908***
Peltoporum africanum	[illegible]	[illegible]	[illegible]	0.113	5	19	D	0.001	17	6	C	0.006	0	7	E	0.715
Rhus leptodictya	[illegible]	[illegible]	[illegible]	2.473	56	25	A	1.365	39	23	B	0.598	100	5	A	4.725*
Strychnos pungens	38	21	B	3.731	15	20	C	0.859	28	104	B	1.080	38	63	B	0.000
Terminalia sericea	0	11	E	2.001	28	18	B	0.243	33	3	-	-	-	0	-	-
Vitex rehmannii	29	24	B	1.067	46	13	A	1.547	86	7	A	0.331	50	4	-	0.061

(Significance Levels : * P < 0.05; ** P < 0.01; *** P < 0.001)

Class A = Highly favoured   Acceptance = 40+
B = Favoured   = 20 - 40
C = Intermediate   = 10 - 20
D = Less favoured   = 5 - 10
E = Non-favoured   = 0 - 5

The foliage of most deciduous trees was still available to the browsers in the early dry season. The species favoured by the kudus remained the same as in the growing season, but with a significant increase in the acceptance of V. rehmannii. The acceptance of R. leptodictya also increased and it became a favoured plant throughout the dry season. The other evergreen species which have much tougher leaves than R. leptodictya remained of low acceptance in the early dry season. In the late dry season when most of the deciduous plants had shed their leaves the kudus significantly increased their acceptance of most species retaining some leaves. The dried leaves of the deciduous species C. molle, T. sericea, and V. rehmannii were of high acceptance to the kudus, but the most noticeable change was the marked increase of the evergreen species S. pungens and T. natalensis. Of these two species S. pungens was the most favoured. Even in the late dry season when food availability was at a minimum the kudus did not eat P. africanum. The dried leaves of D. rotundifolia, B. africanum and O. pulchra were also of low acceptance. In September the new leaves of O. pulchra emerged in advance of most other woody species and were readily eaten by the kudus, the acceptance of these new leaves was 57%.

ii. Impalas

In the growing season the impalas had a high acceptance for G. flavescens, D. cinerea and, unlike the kudus , for A. nilotica and T. sericea (Table 4.6.ii.). A. tortilis was favoured in the late growing season but was of rather low acceptance in the early growing season. The evergreens R. leptodictya and S. pungens were selected in the early growing season when the deciduous plants were still leafing out. By the late growing season the acceptance of these two species had decreased and was similar to that of the intermediate species C. molle and V. rehmannii. Some immature O. pulchra leaves were eaten but generally O. pulchra, B. africana, D. rotundifolia, P. africanum and E. natalensis were of very low acceptance to the impalas during the growing season.

In the early dry season the acceptance of the impalas for D. cinerea and the Acacia species decreased while the acceptance of the broad leaved species C. molle, R. leptodictya and V. rehmannii increased. The species showing an increase in acceptance, plus D. cinerea and G. flavescens, were the favoured species for impalas in the early dry season. The Acacia species, T. sericea and S. pungens were of moderate acceptance and the remaining five species continued to be of low acceptance. The species favoured in the late dry season were similar to those of the early dry season but with the addition of S. pungens and E. natalensis. The acceptance of these two thick leaved evergreen species increased significantly when the availability of deciduous leaves declined. Like the kudus the impalas favoured S. pungens over E. natalensis. The acceptance of the dried leaves of T. sericea also increased.

iii. Goats

In the early growing season the goats had a high acceptance for the two Acacia species, B. africana, D. rotundifolia and O.

pulchra which were only eaten when in new leaf, and for E. natalensis which had been a staple food plant in the dry season and continued to be used in the early months of the growing season. P. africanum, T. sericea and C. molle were of low acceptance to the goats in the early growing season (Table 4.5.iii.). By the late growing season the patterns of acceptance of the goats had changed. The acceptance of B. africana, O. pulchra, D. rotundifolia and E. natalensis had decreased significantly while that of G. flavescens and C. molle had risen significantly. The favoured plants were now C. molle, R. leptodictya, G. flavescens, D. cinerea and V. rehmannii. The Acacia species, T. sericea and E. natalensis were of moderate acceptance and S. pungens, P. africanum and those species eaten only when in new leaf were of low acceptance.

With the onset of the dry season the acceptance of the deciduous plants, D. cinerea and G. flavescens, decreased significantly and the acceptance of E. natalensis rose. The favoured plants in the early dry season were C. molle, R. leptodictya, E. natalensis and particularly V. rehmannii. The microphyllous species, A. nilotica, A. tortilis and D. cinerea were all of low acceptance to the goats in the dry season. In the late dry season the home range of the goats showed signs of depletion. Trees of A. nilotica, A. tortilis, D. cinerea, C. molle and T. sericea nolonger retained many leaves within reach of the goats. The acceptance of E. natalensis increased very significantly. This species together with R. leptodictya and V. rehmannii comprised the favoured species. S. pungens, G.

G. flavescens and D. rotundifolia were also of fairly high acceptance. The goats, in contrast to the kudus and impalas had a higher acceptance for E. natalensis than S. pungens.

iv. Comparison between the Animal Species

Within each season the plants fell into three major groups, favoured, intermediate and non-preferred, based on their acceptance by browsing ungulates; within these groups are some species which are eaten increasingly in the dry season and other which are only eaten when in new leaf. Common woody plant species generally favoured in the early growing season were D. cinerea, G. flavescens, V. rehmannii and the two Acacia species, but the acceptances of the three animal species were not always significantly correlated (Fig 4.6.). The acceptance of the Acacia species by the kudus was lower than that of the other animals, but for V. rehmannii the acceptance of the kudus was higher. T. sericea was of high acceptance to the impalas alone and E. natalensis was favoured only by the goats.

S. africana, O.pulchra and D. rotundifolia were eaten only when in new leaf. These temporary food species were of highest acceptance to the goats and of lowest acceptance to the impalas which ate very little browse at this time of year.

In the late growing season the favoured species remained the same as in the early growing season. The acceptance values of the kudus and goats were significantly correlated, but the impalas still had a lower acceptance for V. rehmannii than did the kudus and goats although the difference was less than in the previous season. The goats had a higher acceptance for C. molle, R. leptodictya and E. natalensis than the impalas and kudus.

The acceptances of woody plant species by kudus and impalas were significantly correlated in the dry season, the goats differed slightly in their selection of plant species. In the early dry season the acceptance of the animals for the Acacia species decreased, D. cinerea, G. flavescens and V. rehmannii remained as favoured species, the impalas now having a high acceptance for the latter species. R. leptodictya was also of high acceptance to all the ungulate species. C. molle was favoured by the impalas and goats but was only of moderate acceptance to the kudus. The goats alone had a high acceptance of T. sericea and the two thick leaved evergreen species, E. natalensis and S. pungens. These species were only eaten by the kudus and impalas in the late dry season when the availability of deciduous leaves was at a minimum.

In the late dry season the favoured plants were the deciduous plants G. flavescens and V. rehmannii which retained the dead leaves on the branches, and the evergreen species R. leptodictya and S. pungens. The goats alone had a high preference for E. natalensis. Of the three evergreen species the animals all had a higher acceptance for the thin leaved R. leptodictya than for the thick leaved species. The kudus and impalas favoured S. pungens over E. natalensis, but for the goats the reverse was true.

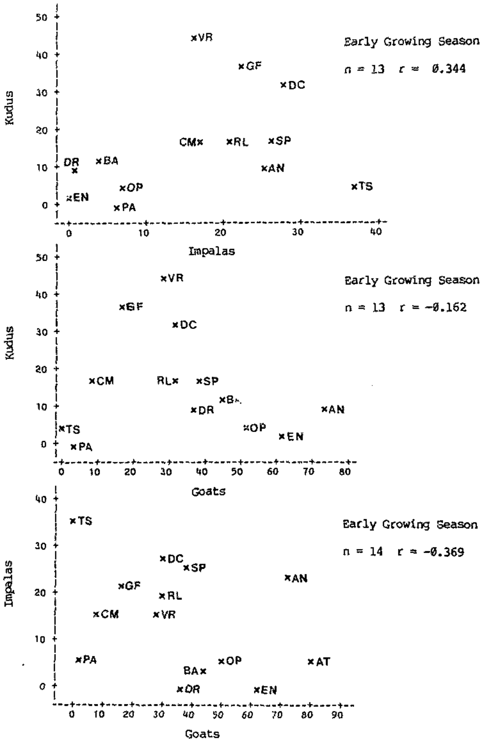


Fig 4.6. A Comparison of the Acceptance of Woody Plant Species by

Kudus, Impalas and Goats.

i. Early Growing Season.

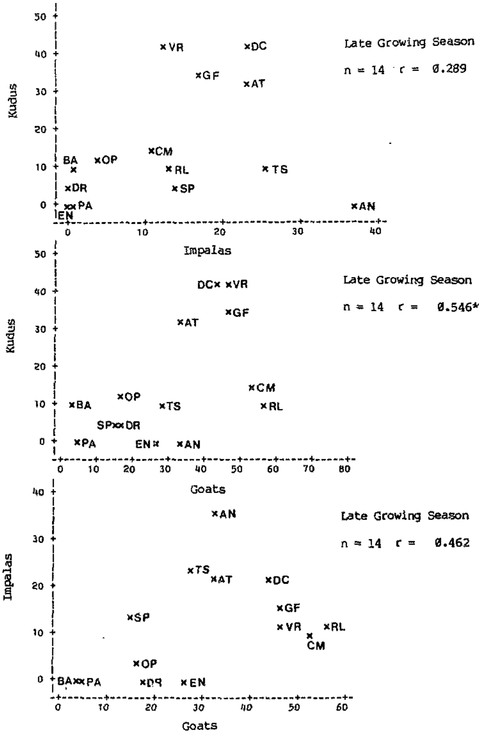


Fig 4.6. A Comparison of the Acceptance of Woody Plant Species by

Kudus, Impalas and Goats.

ii. Late Growing Season.

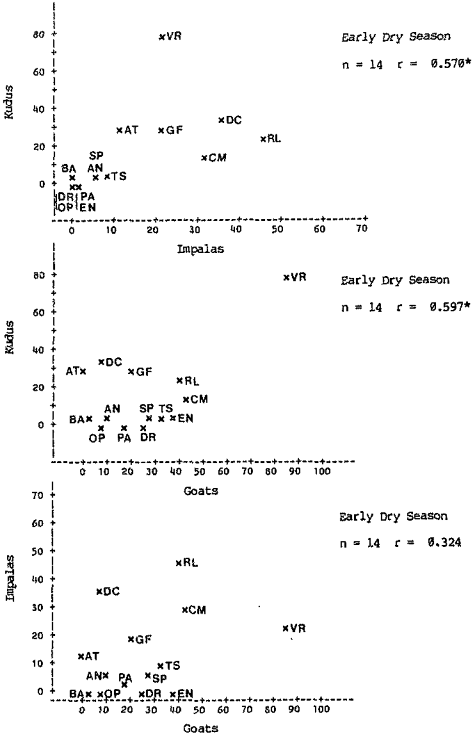


Fig 4.6. A Comparison of the Acceptance of Woody Plant Species by

Kudus, Impalas and Goats.

iii. Early Dry Season.

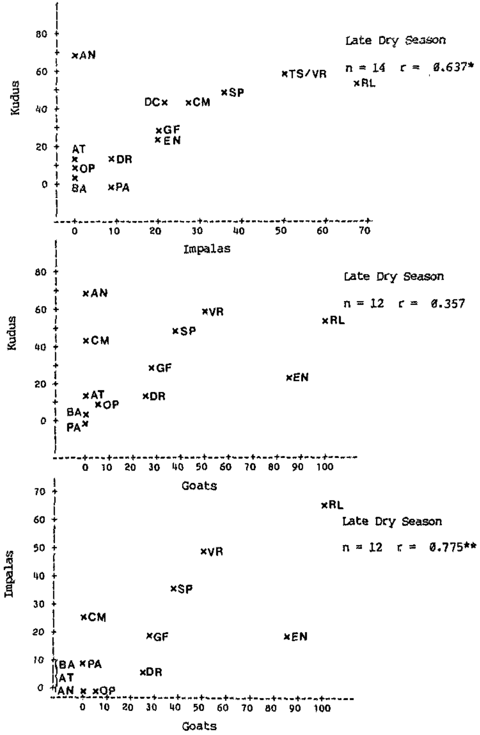


Fig 4.6. A Comparison of the Acceptance of Woody Plant Species by Kudus, Impalas and Goats.

iv. Late Dry Season.

Throughout the year all three ungulate species had a very low acceptance of P. africanum and the mature leaves of B. africana, D. rotundifolia and O. pulchra.

c. The Acceptance Other Woody Plant Species

Several of the less abundant species exhibited high acceptance values, but for many this was probably an effect of small sample size.

i. Kudus

The kudus had a high acceptance for C. zeyheri and E. rigida throughout the growing season (Tables 4.7a.i. & b.i.). The acceptance of S. longipedunculata, Z. mucronata, and S. cocculoides was also high especially in the early growing season. The three less common Grewia species, G. bicolor, G. flava and G. monticola, were of low acceptance as were A. burkei and most of the evergreen species. The kudus continued to favour C. zeyheri in the dry season along with E. menyharthii and S.longipedunculata. In the late dry the acceptance of many woody plant species increased, including that of G. bicolor and G. monticola but not G. flava. The acceptance of several evergreen species increased, the most favoured of which was E. undulata. At the end of the late dry season the first plant to produce new leaves was D. lycioides; although tiny, these leaves were of high acceptance to the kudus.

Table 4.7.a. The Seasonal Acceptance Values of Woody Plant Species Not Chosen for Chemical Analysis

1. Kudus

Species	*Early Growing* Season			Late Growing Season			Early Dry Season			Late Dry Season		
	%Acc	n	Class	%Acc	n	Class	%Acc	n	Class	%Acc	n	Class
Acacia burkei	4	54	E	0	72	E	0	29	E	0	9	E
Acacia karoo	22	18	B	7	14	C	16	61	C	13	8	C
Carissa bispinosa	20	10	B	0	6	E	0	4	-	37	19	B
Combretum zeyheri	43	146	A	56	16	A	53	15	A	71	75	A
Dicapetalum cymosum	0	30	E	0	237	E	0	101	E	0	120	E
Diospyros lycioides	18	103	C	29	100	B	19	73	C	30	21	C
Erythrococca menyharthii	3	34	E	15	26	B	21	14	B	25	12	B
Ehretia rigida	38	13	B	38	13	B	0	28	E	50	6	A
Euclea undulata	25	12	B	0	26	E	0	16	E	47	36	A
Grewia bicolor	37	19	B	0	14	E	0	19	E	29	7	B
Grewia flava	5	20	D	0	49	E	0	30	E	0	8	E
Grewia monticola	7	15	D	0	21	E	0	23	E	61	28	A
Lannea discolor	1	86	E	16	50	C	0	11	E	0	1	-
Lannea edulis	22	24	B	12	4	-	28	1	-	-	-	-
Strychnos cocculoides	36	28	B	17	23	C	0	13	E	0	2	-
Securidaca longipedunculata	41	37	A	15	26	C	33	6	B	25	4	-
Ziziphus mucronata	40	20	A	13	15	C	19	27	C	38	8	B

Class A = Highly favoured Acceptance = 40+

B = Favoured = 20 - 40

C = *Intermediate* = 10 - 20

D = Less favoured = 5 - 10

E = Non-favoured = 0 - 5

Table 4.7.a. The Seasonal Acceptance Values of Woody Plant Species Not Chosen for Chemical Analysis

ii. Impalas

Species	Early Growing Season			Late Growing Season			Early Dry Season			Late Dry Season		
	%Acc	*n*	Class	%Acc	*n*	Class	%Acc	*n*	Class	%Acc	*n*	Class
Acacia burkei	25	72	B	5	38	D	0	18	E	0	2	-
Acacia karoo	40	5	A	0	7	E	22	49	B	0	1	-
Carissa bispinosa	28	29	B	0	12	E	17	6	C	40	20	A
Dicapetalum cymosum	*0*	*229*	*E*	*0*	*124*	*E*	*0*	*163*	*E*	*0*	*56*	*E*
Diospyros lycioides	13	85	C	0	39	E	3	29	E	17	6	C
Erythrococca menyharthii	21	63	B	22	82	B	38	13	B	0	0	E
Ehretia rigida	29	17	B	33	3	-	13	15	C	50	2	-
Euclea undulata	21	19	B	0	4	-	56	24	A	81	21	A
Grewia bicolor	0	20	E	0	19	E	0	30	E	7	13	D
Grewia flava	3	37	E	0	33	E	0	33	E	0	5	E
Grewia monticola	4	26	E	3	40	E	0	39	E	4	23	E
Lannea discolor	29	51	B	4	24	E	0	0	E	0	5	E
Strychnos cocculoides	14	7	C	0	16	E	0	18	E	0	1	-
Securidaca longipedunculata	33	12	B	17	17	C	50	8	A	66	3	-
Ziziphus mucronata	15	20	C	14	22	C	14	17	C	20	5	B

Class A = Highly favoured Acceptance = 40+
B = Favoured = 20 - 40
C = Intermediate = 10 - 20
D = Less favoured = 5 - 10
E = Non-favoured = 0 - 5

Table 4.7.a. The Seasonr' ceptance Values of Woody Plant Species Not Chosen for Chemical Analysis

iii. Goats

Species	Early Growing Season			Late Growing Season			Early Dry Season			Late Dry Season		
	%Acc	n	Class	%Acc	n	Class	%Acc	n	Class	%Acc	n	Class
Acacia burkei	20	10	B	3	33	E	2	55	E	-	-	-
Bridelia mollis	16	16	C	14	7	C	-	-	-	-	-	-
Carissa bispinosa	75	16	A	10	20	C	24	17	B	61	42	A
Dicapetalun cymosum	0	41	E	0	44	E	0	157	E	9	29	D
Diospyros lycioides	8	:1	D	13	24	C	6	32	D	58	29	A
Erythrococca menyharthii	20	64	B	0	13	E	29	7	B	100	1	-
Euclea undulata	40	20	A	67	15	A	11	45	C	70	40	A
Grewia bicolor	35	20	B	0	4	-	26	19	B	0	6	E
Grewia flava	11	53	C	46	13	A	3	33	E	50	2	-
Grewia monticola	53	17	A	20	25	B	27	30	B	38	13	B
Lannea discolor	56	43	A	80	15	A	0	1	-	-	-	-
Strychnos cocculoides	33	12	B	56	16	A	9	22	D	-	-	-

Class A = Highly favoured	Acceptance = 40+
B = Favoured	= 20 - 40
C = Intermediate	= 10 - 20
D = Less favoured	= 5 - 10
E = Non-favoured	= 0 - 5

Table 4.7.b. The Acceptance Values of the Less Common Woody Plant Species Encountered Less than 15 Times in Each Season.

i. Kudus

Species	Growing Season			Dry Season		
	%Acc	n	Class	%Acc	n	Class
Acacia caffra	71	7	A	50	2	-
Acacia hebeclada	50	2	-	-	-	-
Barleria bremekampii	100	1	-	-	-	-
Bequaertiodendron magaliesmontanum	0	1	-	-	-	-
Bridelia mollis	13	8	C	0	5	E
Canthium gilfillanii	0	3	-	0	4	-
Cassine transvaalensis	13	16	C	8	12	D
Combretum apiculatum	75	12	A	50	2	-
Croton gratissimus	0	1	-	50	2	-
Euclea crispa	11	9	C	67	3	-
Gardenia spatulifolia	0	4	-	0	1	-
Maytenus tenuispina	22	18	B	33	12	B
Mundulea sericea	0	6	E	0	3	-
Ozoroa paniculosa	0	20	E	27	22	B
Pappea capensis	10	10	C	80	10	A
Protea welwitschii	50	2	-	-	-	-
Pseudolachnostylis maprouneifolia	100	4	-	0	1	-
Pygmaeothamnus zeyheri	0	17	E	0	13	E
Rhus pyroides	53	15	A	44	9	A
Sclerocarya caffra	5	22	D	0	2	-
Securinega virosa	-	-	-	0	1	-
Strychnos madagascariensis	-	-	-	-	-	-
Tarchonanthus camphoratus	0	1	-	-	-	-
Vangueria infausta	0	2	-	0	2	-
Vitex mombassae	0	4	-	100	1	-
Ximenia caffra	0	15	E	56	18	A

Class A = Highly favoured Acceptance = 40+

B = Favoured = 20 - 40

C = Intermediate = 10 - 20

D = Less favoured = 5 - 10

E = Non-favoured = 0 - 5

Table 4.7.b. The Acceptance Values of the Less Common Woody Plant Species Encountered Less than 15 Times in Each Season.

ii. Impalas.

Species	Growing Season			Dry Season		
	%Acc	n	Class	%Acc	n	Class
Acacia caffra	0	1	A	-	-	-
Acacia hebeclada	-	-	-	-	-	-
Barleria *bremekampi*	-	-	-	-	-	-
Bequaertiodendron magaliesmontanum	-	-	-	-	-	-
Bridelia mollis	0	6	E	33	3	-
Canthium gilfillanii	20	10	C	0	6	E
Cassine transvaalensis	10	10	C	0	11	E
Combretum apiculatum	25	8	B	50	4	-
Combretum zeyheri	0	4	-	18	17	C
Croton gratissimus	-	-	-	-	-	-
Euclea crispa	0	3	-	0	6	E
Gardenia spatulifolia	0	3	-	0	4	-
Lannea edulis	9	11	D	0	7	E
Maytenus tenuispina	9	45	D	0	6	E
Mundulea sericea	0	8	E	0	9	E
Ozoroa paniculosa	8	30	D	0	20	E
Pappea capensis	5	20	D	100	1	-
Protea welwitschii	-	-	-	-	-	-
Pseudolachnostylis maprouneifolia	-	-	-	-	-	-
Pygmaeothamnus zeyheri	0	6	E	-	-	-
Rhus pyroides	25	12	B	66	3	-
Sclerocarya caffra	14	14	C	-	-	-
Securinega virosa	-	-	-	0	2	-
Strychnos madagascariensis	0	2	-	7	14	D
Tarchonanthus camphoratus	-	-	-	-	-	-
Vangueria infaustre	0	5	E	-	-	-
Vitex mombassae	0	2	-	0	7	E
Ximenia caffra	0	17	E	0	6	E

Class A = Highly favoured Acceptance = 40+

B = Favoured = 20 - 40

C = Intermediate = 10 - 20

D = Less favoured = 5 - 10

E = Non-favoured = 0 - 5

Table 4.7.b. The Acceptance Values of the Less Common Woody Plant Species Encountered Less than 15 Times in Each Season.

iii. Goats.

Species	Growing Season			Dry Season		
	%Acc	n	Class	%Acc	n	Class
Acacia caffra	-	-	-	-	-	-
Acacia hebeclada	-	-	-	-	-	-
Acacia karoo	29	7	B	13	15	C
Barleria bremekampi	-	-	-	-	-	-
Bequaertiodendron magaliesmontanum	-	-	-	100	1	-
Bridelia mollis	17	23	C	-	-	-
Canthium gilfillanii	25	12	B	-	-	-
Cassine transvaalensis	8	12	D	14	21	C
Combretum apiculatum	33	6	B	100	2	-
Combretum zeyheri	33	3	-	50	6	A
Croton gratissimus	-	-	-	-	-	-
Euclea crispa	-	-	-	33	5	B
Gardenia spatulifolia	0	1	-	0	1	-
Lannea edulis	-	-	-	-	-	-
Maytenus tenuispina	38	16	A	0	5	E
Mundulea sericea	20	10	B	-	-	-
Ozoroa paniculosa	73	26	A	50	19	A
Pappea capensis	0	1	-	14	7	C
Protea welwitschii	-	-	-	-	-	-
Pseudolachnostylis maprouneifolia	-	-	-	-	-	-
Rhus pyroides	91	11	A	75	12	A
Sclerocarya caffra	0	2	-	-	-	-
Securinega virosa	0	2	-	-	-	-
Strychnos madagascariensis	-	-	-	-	-	-
Tarchonanthus camphoratus	-	-	-	100	1	-
Vangueria infaustra	0	3	-	50	4	-
Vitex mombassae	0	2	-	-	-	-
Ximenia caffra	100	10	A	63	8	A

Class A = Highly favoured	Acceptance = 40+
B = Favoured	= 20 - 40
C = Intermediate	= 10 - 20
D = Less favoured	= 5 - 10
E = Non-favoured	= 0 - 5

ii. Impalas

The impalas had a high acceptance of E. menyharthii and E. rigida in the growing season. L. discolor was favoured when in new eaf, and several thorny species including A. burkei, A. karoo and Z. mucronata were of high acceptance in the early growing season (Tables 4.7.a.ii. & b.ii.). Few of the less abundant woody species were of high acceptance to the impalas in the growing season. Non-preferred species in the growing season included the three Grewia species and the evergreen plants. E. undulata and S. longipedunculata were of high acceptance to the impalas in the dry season. The acceptance of the deciduous species, E. rigida and Z. mucronata, and the evergreen C. bispinosa increased in the late dry season. The acceptance of the three less commom Grewia species remained low.

iii. Goats

L. discolor, Ozoroa paniculosa, S. cocculoides, S. longipedunculata, G. monticola and several other less common woody plants were of high acceptance to the goats in the growing season.(Tables 4.7a.iii. & b.iii.) In the dry season the goats had a high acceptance for Z. mucronata, G. monticola, O. paniculosa and the evergreens C. bispinosa and E. undulata.

iv. Comparison between the Animal Species

The three ungulate species encountered the rare woody species at different frequencies due to the differing proportions of time they spent in each area of the enclosure. In the growing season the goats favoured many rare species. The kudus and impalas had a high acceptance for several species in the early growing season but favoured only two or three species in the late growing season. Generally favoured plants included S. longipedunculata, E. rigida, E. menyharthii, and Acacia species, The kudus and goats also favoured S. cocculoides, and the kudus and impalas favoured Z. mucronata. The kudus alone had a high acceptance for C. zeyheri. The kudus and impalas both had a low acceptance for O. paniculosa, C. bispinosa, L. discolor and the three uncommon Grewia species in the late growing season.

In the dry season the kudus continued to be the only animals to favour C. zeyheri. All the animals showed a high acceptance for E. menyharthii and S. longepedunculata in the early dry season and for Z. mucronata and the evergreens C. bispinosa and E. undulata in the late dry season. The goats favoured a greater variety of woody plants in the early dry season than did the kudus and impalas. These plants included G. bicolor, G. monticola, O. paniculosa and S. cocculoides all of which were of low acceptance to the impalas. The evergreen E. undulata was favoured more by the impalas and goats than by the kudus.

The highly poisonous woody geophyte Dichapetalum cymosum was not eaten by the kudus and impalas. In the late dry season when the new leaves of this species flushed in advance of most other woody plants, the goats however did attempt to eat D. cymosum. The exact acceptance value for this species was not calculated as the goats had to be driven away from these plants for their own safety.

d. The Acceptance of Forb Species Selected for Chemical Anlysis

The forb species selected for chemical analysis were common in 1980-1981 when the goats were studied, but in 1982 when observations on the kudus were made E. alsinoides, O. herbacea and I.macra were much less abundant.

i. Kudus

The kudus had a high acceptance for P. campestris and I. macra in the early growing season. The acceptance of P. campestris decreased in the late growing season but it remained a favoured species (Table 4.8.i.). The acceptance of J. flava increased significantly in the late growing season and it became a favoured species. In the early dry season the kudus continued to select the same species as in the late growing season. The acceptance of S. cordifolia and W. indica increased significantly throughout the dry season until these two species together with H. grisea were the favoured common forbs in the late dry season. With the onset of the growing season the acceptances of these three perennial species decreased significantly. Forb species of low acceptance to the kudus were O. herbacea, E. alsinoides, and S. panduraeforme.

Table 4.8. Comparison between the Seasonal Acceptance Values of Common Forb Species using the 2X2 Contingency Test.

i. Kudus

	Early Growing Season			Diff.	Late Growing Season			Diff.	Early Dry Season			Diff.	Late Dry Season			Diff.
	Acceptance			EGS-LGS	Acceptance			LGS-EDS	Acceptance			EDS-LDS	Acceptance			LDS-EWS
Species	%	n	class	Chi2	%	n	class	Chi2	%	n	class	Chi2	%	n	class	Chi2
Evolvulus alsinoides	0.0	5	E	0.000	0.0	10	E	0.000	0.0	3	-	-	-	0	-	-
Hermannia grisea	4.7	319	C	0.219	5.5	364	C	1.714	8.1	285	C	3.256	14.2	106	B	10.827***
Indigofera macra	22.2	9	A	0.000	0.0	11	E	0.000	0.0	4	-	0.355	6.3	17	C	0.072
Justicia flava	4.7	170	C	16.518***	18.5	205	B	0.025	17.9	140	B	0.667	100.0	1	-	4.037*
Oldenlandia herbacea	-	0	-	-	0.0	3	-	0.000	0.0	2	-	0.000	0.0	2	-	-
Pollichia campestris	23.0	222	A	4.994*	13.9	165	B	0.388	16.5	133	B	0.001	4.2	24	D	3.536
Sida cordifolia	2.0	308	D	2.462	4.0	453	D	13.656***	10.2	501	B	6.890**	19.1	110	B	39.422***
Solanum panduraeforme	0.4	470	E	0.347	0.0	396	E	0.000	0.0	320	E	2.110	3.2	31	D	0.570
Tephrosia forbesii	0.0	34	E	0.000	0.0	39	E	0.669	5.3	57	C	4.418*	0.0	1	-	0.000
Waltheria indica	2.6	655	D	2.508	4.1	776	D	5.707*	6.8	864	C	32.303***	18.4	277	B	71.997***

Class A = Highly favoured   Acceptance = 20+
B = Favoured   = 10 - 20
C = Intermediate   = 5 - 10
D = Less favoured   = 1 - 5
E = Non-favoured   = 0 - 1

(Significance Levels : * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

Table 4.8. Comparison between the Seasonal Acceptance Values of Common Forb Species using the 2X2 Contingency Test.

ii. impalas

Species	Early Growing Season Acceptance			Diff. EGS-LGS	Late Growing Season Acceptance			Diff. LGS-EDS	Early Dry Season Acceptance			Diff. EDS-LDS	Late Dry Season Acceptance			Diff. LDS-EGS
	%	n	class	Chi2	%	n	class	Chi2	%	n	class	Chi2	%	n	class	Chi2
Evolvulus alsinoides	0.5	374	E	0.002	0.9	214	E	0.837	0.0	10	-	-	-	0	-	-
Hermannia grisea	0.9	553	E	3.642	0.0	612	E	48.055***	7.8	716	C	11.319***	2.7	372	D	4.436*
Indigofera macra	1.2	86	D	0.335	1.1	181	D	1.082	0.0	13	-	-	-	0	-	-
Justicia flava	5.6	198	C	2.407	0.0	63	E	0.003	0.0	42	E	23.970***	100.0	2	-	15.597***
Oldenlandia herbacea	0.0	30	E	0.000	0.0	49	E	0.000	0.0	14	E	0.000	0.0	5	E	0.000
Pollichia campestris	7.7	273	C	12.057***	2.1	387	D	29.086***	13.8	145	B	1.405	6.0	50	C	0.015
Sida cordifolia	0.0	501	E	0.170	0.3	776	E	21.831***	3.7	985	D	7.252**	7.1	379	C	34.464***
Solanum panduraeforme	1.7	787	D	3.397	2.9	1292	D	1.727	4.2	530	D	1.915	0.0	69	E	0.316
Tephrosia forbesii	1.6	189	D	2.383	5.0	181	C	18.698***	23.8	63	A	0.399	0.0	1	-	15.167***
Waltheria indica	1.0	1225	D	12.532***	2.9	1515	D	91.559***	11.9	1764	B	0.132	11.3	715	B	105.949***

Class A = Highly favoured — Acceptance = 20+
B = Favoured = 10 - 20
C = Intermediate = 5 - 10
D = Less favoured = 1 - 5
E = Non-favoured = 0 - 1

(Significance Levels : * P < 0.05; ** P < 0.01; *** P < 0.001)

Table 4.6. Comparison between the Seasonal Acceptance Values of Common Forb Species using the 2X2 Contingency Test.

iii. goats

	Early Growing Season Acceptance			Diff. EGS-LGS	Late Growing Season Acceptance			Diff. LGS-EDS	Early Dry Season Acceptance			Diff. EDS-LDS	Late Dry Season Acceptance			Diff. LDS-EWS
Species	%	n	class	Chi2	%	n	class	Chi2	%	n	class	Chi2	%	n	class	Chi2
Evolvulus alsinoides	9.5	189	C	5.552*	4.0	215	D	0.134	5.0	20	C	2.121	0.0	2	-	0.574
Hermannia grisea	16.0	558	B	79.532***	0.6	520	E	94.424***	18.7	427	B	14.611***	32.1	221	C	25.382***
Indigofera macra	1.1	95	D	1.071	3.9	309	D	19.482***	40.0	10	A	-	-	0	-	-
Justicia flava	7.3	96	C	0.209	0.0	14	E	0.765	33.0	3	-	2.452	85.7	56	A	94.200***
Oldenlandia herbacea	2.5	40	D	0.019	0.0	49	E	0.000	0.0	9	E	0.000	0.0	7	E	0.993
Pollichia campestris	34.0	106	A	0.592	28.1	57	A	2.956	16.3	92	B	0.668	33.0	9	A	0.107
Sida cordifolia	0.3	290	E	0.294	0.4	537	E	39.918***	8.9	315	C	5.918*	15.3	287	B	42.991***
Solanum panduraeforme	0.4	262	E	0.015	0.0	204	E	0.000	0.0	87	E	0.194	2.9	35	D	0.338
Tephrosia forbesii	0.0	103	E	48.137***	36.8	204	A	2.651	54.6	22	A	-	-	0	-	-
Waltheria indica	11.1	632	B	6.767**	0.1	1078	E	234.047***	20.2	880	A	5.586*	14.5	318	B	71.658***

Class A = Highly favoured — Acceptance = 20+
B = Favoured — = 10 - 20
C = Intermediate — = 5 - 10
D = Less favoured — = 1 - 5
E = Non-favoured — = 0 - 1

(Significance Levels : * P < 0.05; ** P < 0.01; *** P < 0.001)

ii. Impalas

The impalas also had a high acceptance for P. campestris during the growing season, especially in the early months. Other forbs favoured in the growing season were T. forbesii and S. panduraeforme (Table 4.8.ii.). J. flava was selected in the early growing season and W. indica was of high acceptance in the late growing season. The impalas retained their high acceptance for P. campestris in the early dry season, and the acceptance of T. forbesii increased significantly. The stemmy perennial species W. indica, S. cordifolia and H. grisea also showed a significant increase in acceptance at this time. The acceptance of the latter two species continued to increase in the late dry season and these two plants became the most favoured forbs. The acceptance of the perennial species decreased significantly in the early growing season. Forb species of consistently low acceptance to impalas were E. alsinoides and O. herbacea.

iii. Goats

P. campestris was of high acceptance to the goats in the growing season. They also selected E. alsinoides, especially in the early growing season (Table 4.8.iii.). Other forbs selected in the early growing season were H. grisea and W. indica. The acceptance of these species declined significantly in the late growing season when T. forbesii was of high acceptance. The goats favoured T. forbesii and I. macra in the early dry season. At this time the acceptance of H. grisea, S. cordifolia and W. indica increased significantly. The acceptance of the first two species continued to increase as the dry season progressed but W. indica decreased in acceptance. The favoured forbs in the late dry season were H. grisea, J. flava and P. campestris. With the onset of the growing season the acceptance of S. cordifolia, W. indica and J. flava decreased. The goats had a low acceptance for O. herbacea and S. panduraeforme throughout the year.

iv. Comparison between the Animal Species

All the animals had a high acceptance for P. campestris in the growing season. J. flava was favoured by the impalas in the early growing season and by the kudus in the late growing season. The acceptances of the impalas and goats were significantly correlated in the growing season (Fig 4.7.). Both impalas and goats showed a strong selection for T. forbesii in the late growing season. This species was less common in the following year and the kudus did not favour it. The goats had a high acceptance of the stemmy perennial forbs, H. grisea and W. indica, in the early growing season but generally these species were of highest acceptance to the animals in the dry season.

There was no correlation between the acceptances of the three animal species for forbs in the early dry season although P. campestris was of high acceptance to all the animals. Again the acceptance of the impalas and goats was high for T. forbesii, a species not often encountered by the kudus. In the late dry season the acceptances of kudus and impalas were significantly

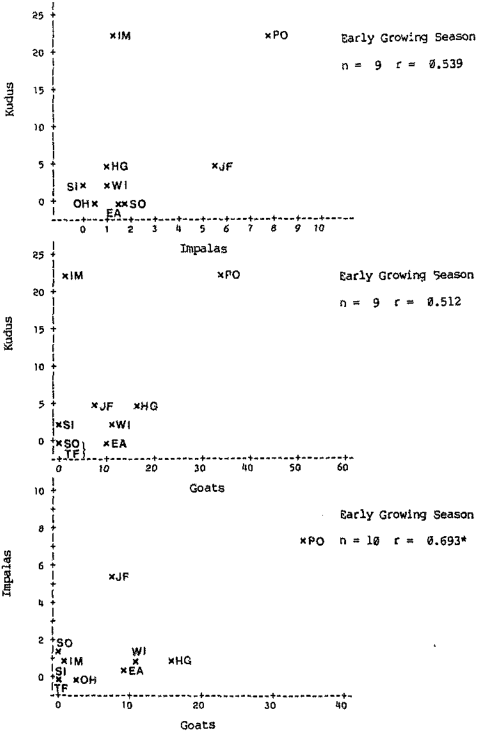


Fig 4.7. A Comparison of the Acceptance of Forb Species by Kudus, Impalas and Goats.

i. Early Growing Season.

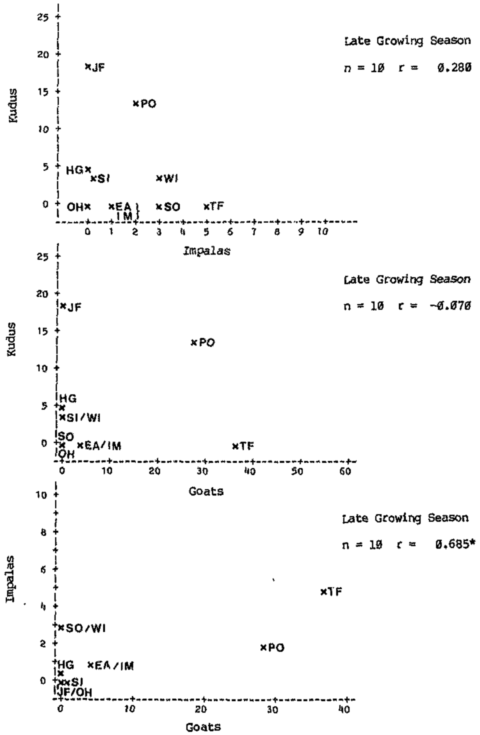


Fig 4.7. A Comparison of the Acceptance of Forb Species by Kudus, Impalas and Goats.

ii. Late Growing Season.

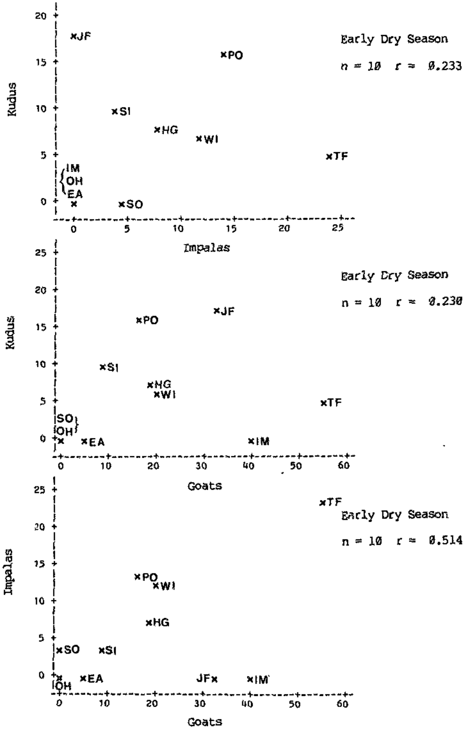


Fig 4.7. A Comparison of the Acceptance . ;orb Species by Kudus, Impalas and Goats.

iii. *Early Dry Season*.

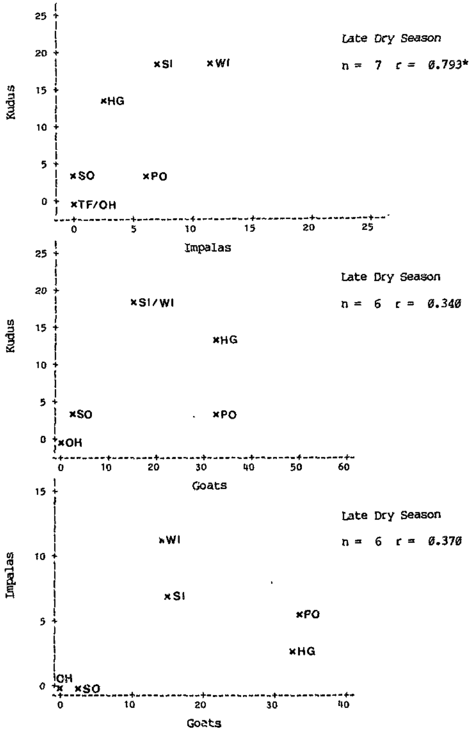


Fig 4.7. A Comparison of the Acceptance of ~~rb~~ Species by Kudus, Impalas and Goats.

iv. Late Dry Season.

correlated. Both had a rather low acceptance of P. campestris in this season. Other than in the early dry season when it was of low acceptance to the impalas J. flava was a favoured forb species in the dry season. All the animals showed a significant increase in the acceptance of the stemmy perennial forbs in the dry season with the goats favouring H. grisea, while the impalas and kudus preferred S. cordifolia and W. indica.

O. herbacea was the only species consistently not eaten by all three ungulate species, E. alsinoides was of very low acceptance to the impalas and kudus, and S. panduraeforme was of low acceptance to the kudus and goats.

e. The Acceptance of Other Forb Species

Many forb species were eaten by the ungulates but were only encountered a few times during the recording sessions.

i. Kudus

Of the more abundant forb species the kudus had a high acceptance for the perennial forb L. javanica and plants of the genus Justicia throughout the growing season (Tables 4.9.a.i. & b.i.). In the early growing season many species were favoured, but of these V. oligocephala was most strongly selected. The acceptamce of J. minima increased significantly (χ^2 10.11 **) in the late growing season then remained high. Fewer forb species were selected in the dry season. The kudus continued to favour L.

Table 4.9.a. The Seasonal Acceptance Values of Forb Species Not Chosen for Chemical Analysis

i. *Kudus*

Species	Early growing Season			Late Growing Season			Early Dry Season			Late Dry Season		
	%Acc	n	Class	%Acc	n	Class	%Acc	n	Class	%Acc	n	Class
Asparagus suavcolens	4	135	D	0	73	E	0	48	E	0	35	E
Blepharis maderaspatensis	6	17	C	4	50	D	0	52	E	0	7	E
Cassia capensis	10	613	B	9	397	C	11	100	B	0	20	E
Chaetacanthus costatus	16	404	B	5	42	C	9	34	C	-	-	-
Commelina africana	10	248	B	8	90	C	8	26	C	-	-	-
Crabbea hirsuta	0	16	E	2	47	D	0	24	E	0	3	-
Elephantorrhiza obliqua	14	386	B	5	59	C	14	7	B	-	-	-
Fadogea monticola	1	295	D	0	22	E	-	-	-	0	18	E
Felicia fascicularis	5	38	C	2	51	D	0	111	E	0	14	E
Hermbstaedtia odorata	10	72	B	9	23	B	0	3	-	-	-	-
Hypoxis obtusa	14	51	B	0	9	E	-	-	-	-	-	-
Indigofera comosa	5	21	C	6	80	C	0	4	-	-	-	-
Indigofera daleoides	0	2	-	0	44	E	0	8	E	0	26	E
Justicia anagalloides	8	170	C	5	21	C	0	2	-	0	3	-
Justicia incerta	4	102	D	10	105	B	10	50	B	0	3	-
Justicia minima	11	210	B	23	139	A	25	122	A	28	80	A
Justicia spergulaefolia	11	73	B	17	30	B	0	5	E	-	-	-
Parinari capensis	0	2	-	0	221	E	0	37	E	0	9	E
Pavonia transvaalensis	6	53	C	11	80	B	20	10	A	0	1	-
Ruellia cordata	9	21	C	0	15	E	0	13	E	0	4	-
Salacia rehmannii	1	77	D	0	1	-	-	-	-	0	4	-
Sida alba	0	14	E	9	32	C	0	18	E	0	1	-
Solanum coccineum	8	33	C	3	38	D	0	7	E	30	8	A
Thunbergia neglecta	3	34	D	0	23	D	0	3	-	-	-	-
Triumfetta sonderi	4	28	D	0	24	E	0	2	-	1	10	D
Vernonia oligocephala	23	198	A	3	38	D	8	12	C	3	35	D

Class A = highly favoured	Acceptance	= 20+
B = Favoured		= 10 - 20
C = Intermediate		= 5 - 10
D = Less favoured		= 1 - 5
E = Non-favoured		= 0 - 1

Table 4.9.a. The Seasonal *Acceptance Values* of *Forb* Species Not Chosen for Chemical Analysis

ii. Impalas

Species	Early growing Season			Late Growing Season			Early Dry Season			Late Dry Season		
	%Acc	n	Class	%Acc	n	Class	%Acc	n	Class	%Acc	n	Class
Acanthosicyos naudiniana	9	23	C	0	15	E	-	-	-	-	-	-
Achranthes sicula	0	96	E	1	537	D	20	60	A	-	-	-
Achyropsis leptostachya	0	14	E	0	23	E	0	14	E	0	2	-
Asparagus suaveolens	12	83	B	3	34	D	0	3	-	0	9	E
Blepharis maderaspatensis	0	45	E	0	275	E	0	67	E	0	1	-
Cassia capensis	4	115	D	0	41	E	0	16	E	0	13	E
Chaetacanthus costatus	22	58	A	0	5	E	-	-	-	0	1	-
Commelina africana	1	247	D	1	124	D	14	57	B	0	15	E
Commelina benghalensis	0	20	E	0	147	E	0	8	E	-	-	-
Commelina eckloniana	0	22	E	0	35	E	0	2	-	0	2	-
Commelina erecta	0	75	E	0	234	E	7	15	C	-	-	-
Crabbea hirsuta	-	2	E	0	5	E	36	45	A	0	2	-
Elephantorrhiza obliqua	3	29	D	0	57	E	0	6	E	0	2	-
Felicia fascicularis	6	80	C	3	35	D	0	35	E	0	21	E
Gomphrena celestioides	2	50	D	0	85	E	0	21	E	100	1	-
Hermbstaedtia odorata	0	32	E	0	58	E	0	20	E	100	1	-
Hibiscus subreniformis	0	57	E	1	96	D	0	2	-	-	-	-
Indigofera daleoides	2	92	D	0	22	E	0	49	C	0	9	E
Indigofera vicioides	0	75	E	0	17	E	-	-	-	-	-	-
Justicia anagalloides	0	75	E	0	10	E	0	3	-	-	-	-
Justicia incerta	7	99	C	0	69	E	0	40	E	-	-	-
Justicia minima	29	99	A	6	31	C	0	20	E	14	29	B
Kohautia virgata	0	30	E	0	22	E	0	4	-	-	-	-
Lippea javanica	16	19	B	6	17	C	6	10	C	22	9	A
Pentarrhinum insipidum	0	33	E	0	95	E	5	22	C	0	2	-
Phyllanthus parvulus	5	99	C	0	77	E	0	1	-	-	-	-
Plumbago zeylanica	6	33	C	7	29	C	50	2	-	-	-	-
Portulaca quadrifida	1	139	D	0	88	E	33	3	-	-	-	-
Pterococcus africana	4	24	D	0	12	E	0	5	E	-	-	-

Table 4.9.a. Continued. . .

Pterococcus africana	4	24	D	0	12	E	0	5	E	-	-	-
Rhynchosia confusa	0	26	E	0	13	E	0	1	-	-	-	-
Rhynchosia venulosa	2	65	D	2	47	D	0	11	E	-	-	-
Ruellia cordata	0	21	E	0	13	E	0	1	-	-	-	-
Schkuhria pinnata	0	34	E	0	162	E	0	14	E	-	-	-
Senecio ineaquidens	0	15	E	0	54	E	0	27	E	0	3	-
Sida alba	0	24	E	0	13	E	0	17	E	0	11	E
Sida *hoepfneri*	0	21	E	0	26	E	0	11	E	-	-	-
Solanum coccineum	4	46	D	2	56	D	0	5	E	0	1	-
Tagetes minuta	2	146	D	0	482	E	0	1	-	-	-	-
Talinum caffrum	0	41	E	0	44	E	0	1	-	-	-	-
Thunbergia neglecta	0	25	E	0	17	E	0	6	E	0	6	E
Triumfetta sonderi	0	25	E	0	17	E	0	6	E	0	6	E

Class A = highly favoured	Acceptance	= 20+
B = Favoured		= 10 - 20
C = Intermediate		= 5 - 10
D = Less favoured		= 1 - 5
E = Non-favoured		= 0 - 1

Table 4.9.a. The Seasonal Acceptance Values of Forb Species Not Chosen for Chemical Analysis

iii. Goats.

Species	Early growing Season			Late Growing Season			Early Dry Season			Late Dry Season		
	%Acc	n	Class	%Acc	n	Class	%Acc	n	Class	%Acc	n	Class
Achranthes sicula	0	73	E	3	389	D	30	20	A	–	–	–
Asparagus saunderiae	0	16	E	0	3	–	0	18	E	0	7	E
Asparagus suaveolens	23	103	A	20	20	A	1	75	D	2	45	D
Borreria scabra	0	21	E	1	148	D	–	–	–	–	–	–
Cassia capensis	0	28	E	29	65	A	–	–	–	–	–	–
Commelina africana	5	170	C	3	40	D	–	–	–	17	12	A
Commelina erecta	0	28	E	1	115	D	–	–	–	–	–	–
Gomphrena celosioides	0	11	E	0	32	E	0	1	–	–	–	–
Hibiscus subreniformis	0	26	E	0	75	E	0	8	E	–	–	–
Indigofera daleoides	0	20	E	19	21	A	67	4	–	50	2	–
Justicia incerta	0	24	E	0	53	E	17	12	B	33	12	A
Pentarrhinum insipidum	14	14	B	24	34	A	0	2	–	0	2	–
Phyllanthus parvulus	1	89	D	0	38	E	–	–	–	–	–	–
Portulaca quadrifida	2	55	D	0	15	E	–	–	–	–	–	–
Pterococcus africana	0	16	E	11	18	B	60	5	A	–	–	–
Rhynchosia confusa	6	16	C	9	22	C	0	3	–	100	1	–
Rhynchosia venulosa	0	25	E	13	24	B	0	1	–	–	–	–
Senecio ineaquidens	8	12	C	27	26	A	0	4	–	0	4	–
Solanum coccineum	7	30	C	0	16	E	10	10	B	50	4	–
Tagetes minuta	0	85	E	0	130	E	–	–	–	–	–	–

Class A = highly favoured Acceptance = 20+
B = Favoured = 10 – 20
C = Intermediate = 5 – 10
D = Less favoured = 1 – 5
E = Non-favoured = 0 – 1

Table 4.9.b. The Acceptance Values of Species of Forb Species Encountered Less than 15 Times in Each Season.

i. Kudus

Species	Growing Season			Dry Season		
	%Acc	n	Class	%Acc	n	Class
Acalypha petiolaris	0	2	-	-	-	-
Acanthosicyos naudiniana	-	-	-	0	4	-
Achyranthes sicula	-	-	-	0	10	E
Achyropsis leptostachya	5	19	C	10	10	B
Agathisanthemum bojeri	31	13	A	4	25	D
Aloe davyana	20	5	A	0	7	E
Anthericum cooperi	0	1	-	-	-	-
Antizoma harveyana	0	14	E	0	7	E
Asclepias fruticosa	0	1	-	-	-	-
Asparagus buchananii	8	38	C	0	9	E
Asparagus saunderiae	0	16	E	0	11	E
Beolum angustifolium	6	17	C	11	9	B
Bauhinia macrantha	10	57	B	9	11	C
Boophane disticha	50	6	A	-	-	-
Borreria scabra	0	1	-	0	4	-
Bulbine angustifolia	0	8	E	0	1	-
Cleome maculata	-	-	-	0	1	-
Commelina erecta	5	38	C	0	4	-
Commelina eckloniana	4	25	D	-	-	-
Corchorus kirkii	0	8	E	0	2	-
Crotilaria pisicarpa	-	-	-	0	6	E
Cyanotis speciosa	0	6	-	-	-	-
Cryptolepis oblongifolia	0	2	-	-	-	-
Dicerocaryum zanguebarium	-	-	-	0	5	E
Dicoma macrocephala	-	-	-	0	11	E
Dipcardi viride	-	-	-	0	1	-
Euphorbia inaequilatera	0	3	-	-	-	-
Felicia muricata	-	-	-	0	22	E
Gladeolus calcaratus	100	1	-	0	4	-
Gomphrena celosioides	0	5	E	0	17	E
Helichrysum kraussii	0	3	-	-	-	-

Table 4.9.b. Continued. . .

Hibiscus subreniformis	0	3	-	0	7	E
Hemizigia canescens	36	11	A	-	-	-
Hermannia boraginiflora	3	31	D	0	10	E
Indigofera daleoides	0	46	E	0	34	E
Indigofera nebrowniana	0	1	-	33	6	A
Indigofera sordida	16	19	B	0	2	-
Indigofera vicioides	17	6	B	0	2	-
Ipomea *obscura*	4	23	D	0	1	-
Ipomea ommaneyi	25	4	-	-	-	-
Jatropha zeyheri	0	2	-	0	7	E
Kalanchoe paniculata	-	-	-	0	3	-
Kohautia *virgata*	0	3	-	0	5	E
Ledebouria graminifolia	-	-	-	0	1	-
Limium fenestratum	-	-	-	0	1	-
Lippea javanica	28	29	A	50	28	A
Lantana rugosa	14	14	B	0	5	E
Melhania prostrata	0	6	E	0	17	E
Merremia tridentata	17	18	B	0	2	-
Monchema divaricatum	-	-	-	0	1	-
Nidorella resedifolia	-	-	-	0	1	-
Ocimum canum	-	-	-	56	9	A
Opuntia ficus indica	14	7	B	0	10	E
Oxalis corniculata	0	2	-	0	3	-
Parvetta zeyheri	0	19	E	-	-	-
Pellaea colomelanos	0	2	-	0	5	E
Pentarrhinum insipidum	0	12	E	0	17	E
Phyllanthus parvulus	-	-	-	0	7	E
Plumbago zeylanica	0	2	-	48	29	A
Polygala sphenoptera	0	1	-	0	14	E
Portulaca quadrifida	0	2	-	0	6	E
Pterococcus africanus	-	-	-	0	1	-
Raphionacme burkei	33	3	-	-	-	-
Rhoicissus tridentata	0	9	E	-	-	-
Rhynchosia confusa	0	2	-	0	4	-
Rhynchosia longiflora	11	9	B	29	7	A

Table.4.9.b. Continued. . .

Rhynchosia venulosa	8	12	E	Ø	35	E
Schkuhria pinnata	17	42	B	Ø	2	-
Senecio inaequidens	11	15	B	-	-	-
Senecio venosus	11	46	B	-	-	-
Sida ovata	4	27	D	Ø	2	-
Sida rhomboidifolia	-	-	-	Ø	1Ø	E
Solanum seaforthianum	1ØØ	1	-	-	-	-
Sphedamnocarpus pruriens	13	8	B	-	-	-
Sutera burkeana	17	6	B	Ø	1	-
Tagetes minuta	Ø	1	-	-	-	-
Tephrosia lupinifolia	8	13	C	-	-	-
Tephrosia longipes	Ø	1Ø	E	-	-	-
Tribulus terrestris	-	-	-	Ø	1	-
Triumfetta pentandra	7	14	C	7	29	C
Trochomeria macrocarpa	-	-	-	Ø	27	E
Turbina oblongata	-	-	-	Ø	1	-
Vernonia staehelinoides	-	-	-	Ø	2	-
Unidentified 1	33	3	-	-	-	-
Unidentified 2	Ø	1	-	1ØØ	1	-
Unidentified 3	1ØØ	1	-	-	-	-

Plus 18 unidentified species encountered only once or twice and not seen to be eaten.

Class A	= highly favoured	Acceptance = 2Ø+
B	= Favoured	= 1Ø - 2Ø
C	= Intermediate	= 5 - 1Ø
D	= Less favoured	= 1 - 5
E	= Non-favoured	= Ø - 1

Table 4.9.b. The Acceptance Values of Species of Forb Species Encountered Less than 15 Times in Each Season.

ii. Impalas

Species	Growing Season			Dry Season		
	%Acc	n	Class	%Acc	n	Class
Acalypha petiolaris	0	1	-	-	-	-
Agathisanthemum bojeri	0	13	E	50	4	-
Aloe davyana	0	1	-	-	-	-
Amaranthus thunbergii	-	-	-	0	1	-
Anthericum galpinii	0	2	-	-	-	-
Antizoma harveyana	0	5	E	-	-	-
Asclepias burchellii	0	11	E	0	2	-
Asclepias fruticosa	0	22	E	-	-	-
Asparagus buchananii	0	10	E	20	5	A
Asparagus saunderiae	0	20	E	0	6	E
Becium angustifolium	14	28	B	9	23	C
Bauhinia macrantha	0	8	E	0	6	E
Bidens bipinnata	0	2	-	-	-	-
Boophane disticha	0	2	-	-	-	-
Borreria scabra	-	-	-	0	3	-
Brayulinea densa	0	33	E	67	12	A
Bulbine angustifolia	0	3	2	0	2	-
Cleome maculata	0	8	E	0	1	-
Ceratotheca triloba	0	1	-	-	-	-
Commelina livingstonei	0	5	-	-	-	-
Conyza floribunda	0	3	-	-	-	-
Corchorus kirkii	0	16	E	0	3	-
Crotilaria pisicarpa	0	40	E	0	4	-
Cyanotis speciosa	0	16	E	-	-	-
Cyphocarpa angustifolia	0	2	-	-	-	-
Dicerocaryum zanguebarium	0	26	E	5	40	C
Dicoma macrocephala	0	9	E	0	2	-
Dipcardi marlothii	0	1	-	-	-	-
Dipcardi viride	0	2	-	-	-	-
Euphorbia inaequilatera	0	5	E	-	-	-

Table 4.9.b. Continued. . .

Pe· · › monticola	0	6	E	0	17	E
Peli.!. muricata	12	17	B	0	15	E
Gladeolus calcaratus	0	11	E	0	2	-
Gomphrena celosioides	0	5	E	0	17	E
Hemizio! · ·escens	0	1	-	-	-	-
Hemizig. · · ·ensis	0	1	-	0	2	-
Hermannia boraginiflora	6	18	C	0	3	-
Hibiscus meeusei	40	5	A	0	2	-
Hypoxis obtusa	0	1	-	-	-	-
Indigofera comosa	0	4	-	-	-	-
Indigofera distir ·ha	-	-	-	0	1	-
Indigofera filipes	0	14	E	-	-	-
Indigopera nebrowniana	0	6	E	0	4	-
Indigofera sordida	0	4	-	-	-	-
Ipomea obscura	3	29	D	-	-	-
Ipomea ornaneyi	0	4	-	25	8	A
Jatropha zeyheri	4	25	D	-	-	-
Justicia spergulaefolia	13	8	A	0	2	-
Kalanchoe paniculata	0	10	E	0	13	E
Ledebouria graminifolia	0	2	-	-	-	-
Leucas neuflizeana	-	-	-	0	4	-
Limeum fenestratum	0	3	-	-	-	-
Limeum viscosum	0	1	-	-	-	-
Lantana rugosa	4	25	D	0	13	C
Lophiocarpus tenuissimus	0	3	-	-	-	-
Melhania prostrata	0	2	-	0	3	-
Merremia tridentata	9	3?	C	0	12	E
Nidorella resedifolia	0	2	-	0	2	-
Ocimum canum	0	16	E	0	4	-
Opuntia ficus-indica	0	15	E	0	12	E
Oxygonium dregeanum	0	18	E	-	-	-
Oxygonium sinuatum	0	3	-	-	-	-
Pellaea calomelanos	0	5	E	0	1	-
Phyllanthus maleraspatensis	0	11	E	-	-	-

Table 4.9.b. Continued. . .

Polygala sphenoptera	6	47	C	0	1	-
Pterococcus africana	3	36	D	0	5	E
Raphionacme burkei	0	3	-	-	-	-
Rhynchosia longiflora	0	1	-	0	3	-
Rhynchosia monophylla	0	1	-	-	-	-
Rhynchosia rinenosa	0	11	E	-	-	-
Ruellia malacophylla	0	1	-	-	-	-
Ruellia patula	0	1	-	-	-	-
Salacia rehmannii	0	1	-	25	4	-
Senecio longifolia	0	2	-	-	-	-
Senecio venosus	-	-	-	0	12	E
Sida chrysantha	100	1	-	0	2	-
Sida ovata	0	1	-	-	-	-
Sida pseudocordifolia	0	2	-	-	-	-
Sida rhomboidifolia	-	-	-	0	17	E
Solanum incanum	9	11	C	-	-	-
Solanum seaforthianum	0	1	-	-	-	-
Sphedamnocarpus pruriens	0	3	-	0	4	E
Striga asiatica	0	1	-	-	-	-
Striga gesnerioides	0	1	-	-	-	-
Stylosanthes fruticosa	0	6	E	0	3	-
Sutera burkeana	0	1	-	-	-	-
Tephrosia longipes	0	3	-	0	1	-
Tribulus terrestris	0	32	E	0	1	-
Triumfetta pentandra	0	4	-	0	1	-
Vernonia fastigiata	0	3	-	-	-	-
Vernonia monocephala	0	1	-	-	-	-
Vernonia oligocephala	14	7	B	7	14	C
Vernonia poskeana	-	-	-	0	19	E
Zinnea multiflora	0	8	E	0	1	-
Zornia capensis	0	1	-	-	-	-

Plus 55 unidentified species encountered only once or twice and not seen to be eaten.

Class A = highly favoured	Acceptance	= 20+
B = Favoured		= 10 - 20
C = Intermediate		= 5 - 10
D = Less favoured		= 1 - 5
E = Non-favoured		= 0 - 1

Table 4.9.b. The Acceptance Values of Species of Forb Species Encountered Less than 15 Times in Each Season.

iii. Goats

Species	Growing Season			Dry Season		
	%Acc	n	Class	%Acc	n	Class
Achyropsis leptostachya	27	15	A	36	22	B
Acalypha petiolaris	0	1	-	-	-	-
Acanthosicyos naudiniana	0	8	E	-	-	-
Agathisanthemum bojeri	0	15	E	0	1	-
Aloe davyana	0	1	-	-	-	-
Anthericum *galpinii*	-	-	-	0	1	-
Asclepias burchellii	25	4	-	-	-	-
Asclepias fruticosa	26	23	A	-	-	-
Asparagus buchananii	14	21	B	-	-	-
Becium angustifolium	53	15	A	-	-	-
Bauhinia macrantha	40	5	A	-	-	-
Brayu*linea densa*	0	2	-	-	-	-
Cassia absus	0	5	E	-	-	-
Cleome maculata	80	5	A	-	-	-
Commelina benghalensis	0	54	E	-	-	-
Commelina eckloniana	0	26	E	-	-	-
Corchorus *kirkii*	0	9	E	-	-	-
Crabbea hirsuta	0	10	E	63	5	A
Crotilaria sphaerocarpa	0	1	-	-	-	-
Cyanotis speciosa	0	4	-	-	-	-
Cyphocarpa angustifolia	0	2	-	-	-	-
Dicerocaryum zanguebarium	0	5	E	0	4	-
Dicoma macrocephala	0	14	E	50	2	-
Elephantorrhiza oblique	0	3	-	-	-	-
Euphorbia inaequilatera	0	22	E	0	3	-
Fadogea monticola	-	-	-	0	1	-
Felicia fascicularis	5	40	C	9	22	C
Felicia muricata	0	8	E	14	7	B
Gladeolus calcaratus	50	4	-	-	-	-
Hermbstaedtia odorata	27	22	A	-	-	-
Hermannia boraginiflora	0	15	E	-	-	-

Table 4.9.b. Continued. . .

Hibiscus meeusei	0	6	E	-	-	-
Hypoxis obtusa	25	4	-	-	-	-
Indigofera comosa	0	1	-	-	-	-
Indigofera distincha	-	-	-	0	1	-
Indigofera nebrowniana	0	1	-	-	-	-
Indigofera sordida	0	1	-	-	-	-
Ipomea ommaneyi	0	4	-	25	8	A
Jatropha zeyheri	0	9	E	0	2	-
Justicia anagalloides	0	39	E	-	-	-
Justicia spergulaefolia	0	15	E	0	26	E
Kalanchoe paniculata	18	22	B	0	1	-
Kohautia virgata	4	24	-	-	-	-
Limeum fenestratum	0	1	-	-	-	-
Lippea javanica	0	15	E	17	12	B
Lantana rugosa	14	7	B	-	-	-
Melhania prostrata	33	3	-	-	-	-
Merremia tridentata	71	17	A	-	-	-
Nidorella resedifolia	67	3	-	0	1	-
Ocimum canum	0	6	E	-	-	-
Opuntia ficus-indica	0	7	E	0	12	E
Oxalis corniculata	0	4	-	-	-	-
Pavonia transvaalensis	0	32	E	-	-	-
Pellaea colomelanos	-	-	-	0	1	-
Plumbago zeylanica	0	15	D	-	-	-
Polygala sphenoptera	0	22	E	0	1	-
Raphionacme burkei	0	1	-	-	-	-
Rhynchosia longiflora	33	3	-	-	-	-
Rhynchosia densiflora	0	1	-	-	-	-
Ruellia cordata	0	6	E	0	1	-
Salacia rehmannii	0	2	-	-	-	-
Schkuhria pinnata	0	20	E	-	-	-
Sida alba	9	11	C	-	-	-
Sida chrysantha	0	3	-	-	-	-
Sida hoepfneri	0	40	E	0	9	E
Sida ovata	0	1	-	-	-	-

Table 4.9.b. Continued. . .

Sida pseudocordifolia	0	1	-	-	-	-
Sida rhomboidifolia	-	-	-	0	1	-
Solanum incanum	25	8	A	0	2	-
Solanum seaforthianum	0	1	-	-	-	-
Stylosanthes fruticosa	0	31	E	-	-	-
Talinum caffrum	7	15	C	-	-	-
Thesium cytisioides	0	1	-	-	-	-
Tephrosia longipes	0	2	-	-	-	-
Tephrosia lupinifolia	0	1	-	-	-	-
Thunbergia neglecta	0	24	E	-	-	-
Triumfetta sonderi	0	10	E	14	7	B
Vernonia fastigiata	0	2	-	-	-	-
Vernonia oligocephala	33	3	-	100	1	-
Vernonia poskeana	0	6	E	-	-	-
Vernonia staehelinoides	0	1	-	-	-	-
Zinnea multiflora	0	8	E	-	-	-
Unidentified 1	-	-	-	100	1	-
Unidentified 2	-	-	-	100	1	-
Unidentified 3	-	-	E	100	1	-

Plus 22 unidentified species encountered only once or twice and *not seen* to be eaten.

Class A = highly favoured	Acceptance = 20+	
B = Favoured		= 10 - 20
C = Intermediate		= 5 - 10
D = Less favoured		= 1 - 5
E = Non-favoured		= 0 - 1

javanica and J. minima. Other forbs favoured in the early dry season were P. transvaalensis, C. capensis and Justicia incerta. Forb species of consistantly low acceptance to the kudus were A. suaveolens, Triumphetta sonderi, Fadogea monticola and Felicia fascularis.

ii. Impalas

The impalas exhibited the highest acceptance for J. minima in the early growing season (x2 5.58 *); in the late growing season this species was of intermediate acceptance. Other species selected in the early growing season were C. costatus, Becium angustifolia, L. javanica and A. suaveolens (Tables 4.9.a.ii & b.ii.). In the late growing season only Pterococcus africana and M. tridentata were of high acceptance to the impalas. In the early dry season the impalas increased their acceptance of Brayulinea densa (x2 15.65 ***) and Achyanthes spicula (x2 75.53 ***). Crabbea hirsuta was also favoured. In the late dry season few forbs were selected, in this season L. javanica and J. minima were the favoured forbs. Species not eaten by the impalas included Blepharis maderaspatensis, Sida alba, Sida hoepfneri, Achyranthes leptostachya and many less common species.

iii. Goats

Few forb species were of high acceptance to the goats (Tables 4.9.a.iii. & b.iii.). A. suaveolens and Pentarrhinum insipidum were favoured throughout the growing season. In the late growing season C. capensis and Senecio inaequidens were also selected. The goats had a moderate acceptance in the late growing season for two species known to be toxic to livestock, Kalanchoe paniculata and Asclepias fruticosa. The goats had a high acceptance for J. incerta, A. spicula and B. maderaspatensis in the early dry season, even though all three of these species had been of very low acceptance in the growing season. In the late dry season the goats ate few forbs but continued to favour J. incerta.

iv. Comparison between the Animal Species

Between the animals the encounter rates with individual forb species varied greatly due to both area selection differences and to the differences in the species composition in the two years of the study. In the growing season the kudus and impalas favoured L. javanica and Justicia species, especially J. minima. The goats had a lower acceptance for Justicias and rarely encountered L. javanica. The impalas and goats favoured A. suaveolens but the kudus has a low acceptance for this thorny forb. The goats had a moderate acceptance in the late growing season for K. paniculata and A. fruticosa known to be toxic to livestock. These two species were rejected by the impalas which encountered these plants at a similar frequency as the goats. The kudus rarely came into contact with these species.

In the dry season many forb species died down. The kudus and impalas continued to favour L. javanica and J. minima. The forb A. spicula was favoured by both the impalas and goats in the dry but was not often encountered by the kudus.

4.3.5. Species Selection: Feeding Duration

a. Common Woody Plants

The animals rarely ate from one plant or a group of individuals of species for more than five minutes, even when feeding on tree or clump of bushes. The variation in the time spent feeding on plants within the same species was great.

i. Kudus

The kudus rarely fed for longer than an average of 40 seconds on individual plants of any species. In the early growing season the average duration of feeding was greatest on G. flavescens, C. mol' and the evergreen S. pungens (Table 4.10.i.). The maximum time spent eating any one plant was five minutes for G. flavescens. A few plants of D. cinerea and S. pungens were eaten for up to three minutes. R. leptodictya was fed on for an average of 70 seconds in the late growing season. Other favoured species were D. cinerea, G. flavescens and V. rehmannii. The maximum feeding duration recorded in this season was six minutes on D. cinerea and G. flavescens. Plants eaten for less than an average of ten seconds in the growing season were E. natalensis and P. africanum.

Table 4.10. Duration of Feeding (seconds) on Individual Woody *Plants*.

i. Kudus

Species	Early Growing Season				Late Growing Season				Early Dry Season				Late Dry Season			
	Rank	Mean±SE	Max	n	Rank	Mean±SE	Max	n	Rank	Mean±SE	Max	n	Rank	Mean±SE	Max	n
Acacia nilotica	10.5	10 ± 6	15	2	-	0 ± -	0	0	5	32 ±16	65	3	10	19 ±10	58	5
Acacia tortilis	-	0 ± -	0	0	6.5	20 ± 8	43	4	8	22 ±12	120	9	13	2 ± -	2	1
Burkea africana	9	11 ± 1	44	64	6.5	20 ± 4	93	30	11	16 ± 4	53	12	11	17 ± 3	27	5
Combretum molle	2	33 ± 8	150	18	8.5	15 ± 5	53	12	3	34 ±10	75	7	9	21 ± 3	76	28
Dichrostachys *cinerea*	4	29 ± 5	204	51	2	57 ± 7	364	99	2	36 ± 6	193	61	12	9 ± 2	12	3
Dombeya rotundifolia	5	24 ±11	163	14	10.5	8 ± 2	13	5	13	2 ± -	2	1	6	30 ± 6	80	12
Euclea natalensis	12	8 ± 2	9	2	-	0 ± -	0	0	10	21 ± 7	38	4	8	23 ± 5	102	28
Grewia flavescens	3	32 ± 3	298	189	4	31 ± 3	372	176	10	21 ± 7	38	4	8	23 ± 5	120	28
Ochna pulchra	8	12 ± 2	99	88	8.5	15 ± 1	72	120	8	22 ± -	22	1	4	36 ± 5	242	47
Peltophorum africanum	-	0 ± -	0	0	-	0 ± -	0	0	-	0 ± -	0	0	-	0 ± -	0	0
Rhus leptodictya	7	14 ± 9	31	3	1	70 ±64	134	2	8	22 ± 7	50	6	1	121 ±47	293	6
Strychnos pungens	1	34 ± 8	198	26	10.5	8 ± 4	20	4	12	7 ± 2	9	2	2	46 ± 8	521	81
Terminalia sericea	10.5	10 ± 2	19	7	5	21 ± 8	69	8	6	31 ±20	70	3	3	39 ± 9	76	15
Vitex rehmannii	6	23 ± 5	157	40	3	30 ± 9	95	13	1	37 ± 6	172	39	5	31 ± 8	92	13

Table 4.10. Duration of Feeding (seconds) on Individual Woody Plants.

ii. Impalas

Species	Early Growing Season				Late Growing Season				Early Dry Season				Late Dry Season			
	Rank	Mean±SE	Max	n	Rank	Mean±SE	Max	n	Rank	Mean±SE	Max	n	Rank	Mean±SE	Max	n
Acacia nilotica	5	14 ± 4	51	14	6	25 ± 5	160	35	4	47 ±16	235	15	–	0 ± –	0	0
Acacia tortilis	13	3 ± 0	3	2	1	54 +20	248	16	6	35 +18	221	12	–	0 + –	0	0
Burkea africana	10	8 ± 4	25	5	9	10 ± –	10	1	–	0 ± –	0		–	0 ± –	0	0
Combretum molle	12	6 ± 1	17	18	2	53 ±21	193	9	8.5	23 ± 6	72	11	3	30 ±12	180	14
Dichrostachys cinerea	4	17 ± 3	77	56	3	50 ±10	349	54	2	57 ±11	326	46	9	8 ± 3	10	2
Dombeya rotundifolia	3	18 ±15	48	3	–	0 ± –	0	0	–	0 ± –	0	0	10	3 ± –	3	1
Euclea natalensis	–	0 ± –	0	0	–	0 ± –	0	0	–	0 ± –	0	0	7	19 ± 4	84	22
Grewia flavescens	1	20 ± 3	191	97	4	45 ± 7	201	64	8.5	23 ± 3	182	93	8	12 ± 2	79	57
Ochna pulchra	9	9 ± 1	29	31	8	12 ± 8	79	13	–	0 ± –	0	0	11	2 ± –	2	1
Peltophorum africanum	11	7 ± 3	14	4	7	19 ± –	19	1	5	38 ± –	38	1	2	45 ±35	113	3
Rhus leptodictya	6.5	12 ± 3	23	6	10	7 ± 3	16	4	8.5	23 ± 6	48	5	5	26 ± 4	30	2
Strychnos pungens	2	19 ± 5	25	12	12	3 ± 3	5	2	1	60 ±52	164	3	6	21 ± 3	100	59
Terminalia sericea	8	10 ± 3	59	10	5	29 ± 6	59	11	8.5	23 ±14	36	2	1	48 ±16	82	4
Vitex rohmannii	6.5	12 ± 1	13	2	11	5 ± 1	6	2	3	53 ± 4	146	7	4	20 ±14	95	6

Table 4.10. Duration of Feeding (seconds) on Individual Woody Plants.

iii. Goats

Species	Early Growing Season				Late Growing Season				Early Dry Season				Late Dry Season			
	Rank	Mean±SE	Max	n	Rank	Mean±SE	Max	n	Rank	Mean±SE	Max	n	Rank	Mean±SE	Max	n
Acacia nilotica	2	34 ±13	121	9	5	40 ±15	84	6	12	18 ± 5	27	3	–	0 ± –	0	0
Acacia tortilis	9.5	17 ±10	47	4	13	13 ± –	13	1	–	0 ± –	0	0	–	0 ± –	0	0
Burkea africana	7.5	18 ± 3	130	70	11.5	15 ±11	25	2	9	32 ±16	48	2	–	0 ± –	0	0
Combretum molle	11.5	15 ± 6	30	4	3	47 ±10	83	9	4	44 ±16	350	20	–	0 ± –	0	0
Dichrostachys cinerea	5	25 ± 5	95	26	6	39 ± 9	121	19	8	35 ± 9	44	2	–	0 ± –	0	0
Dombeya rotundifolia	3	31 ± 7	256	37	11.5	15 ± 3	32	9	3	52 ±11	206	24	2	27 ± 9	106	11
Euclea natalensis	1	42 ± 4	207	90	8	34 ±15	240	16	6	37 ± 7	468	89	1	57 ± 5	504	243
Grewia flavescens	6	19 ± 3	60	53	2	81 ±12	722	113	7	36 ± 4	150	73	6	17 ± 4	109	53
Ochna pulchra	9.5	17 ± 2	104	130	9	31 ± 8	116	24	13	14 ± 2	38	16	7	9 ± 4	20	4
Peltophorum africanum	7.5	18 ± 7	25	2	14	9 ± –	9	1	10	25 ± –	25	1	–	0 ± –	0	0
Rhus leptodictya	13	8 ± 2	14	6	10	27 ± 5	68	14	1	140 ±76	643	3	3	24 ±13	74	5
Strychnos pungens	11.5	15 ± 4	39	8	4	42 ±31	168	5	11	20 ± 4	109	29	5	16 ± 5	82	24
Terminalia sericea	–	0 ± –	0	0	7	35 ±13	81	5	5	38 ± –	38	1	–	0 ± –	0	0
Vitex rehmannii	4	27 ±10	78	7	1	104 ±36	234	6	2	58 ±23	156	6	4	22 ±10	32	2

In the early dry season . ny species were eaten by the kudus for an average of 30-40 seconds. The evergreens and A. tortilis, B. africana, D. rotundifolia and O. pulchra were of shorter feeding duration. Again the longest individual feeding times were recorded on D. cinerea and G. flavescens. The duration of feeding on the evergreen species R. leptodictya and S. pungens increased in the late dry season, but the average time spent on plants of B. africana and the microphyllous species was very low. The longest time the kudus were recorded feeding on any one plant was nine minutes on S. pungens in the late dry season.

ii. Impalas

The average feeding duration by impalas on woody plants was generally less than half a minute in the early growing season. Only plants of G. flavescens were eaten for longer, up to three minutes on a few occasions (Table 4.10.ii.). In the late growing season the impalas continued to favour G. flavescens along with C. molle, D. cinerea and A. tortilis. The longest feeding duration recorded in this season was six minutes for D. cinerea. The evergreen E.natalensis, and those species generally eaten only when in new leaf, were rarely eaten for more than ten seconds by the impalas.

S. pungens plants were eaten for an average of 60 seconds in the early dry season. The Acacia species, D. cinerea, V. rehmannii and P. africanum were also favoured. The longest individual feeding durations were on D. cinerea and the two Acacia species.

In the late dry season the deciduous plants C. molle, T. sericea and P. africanum were eaten for longest by the impalas. The maximum time spent feeding on any one of these plants was two to three minutes.

iii. Goats

In the early growing season the goats fed for more than 30 seconds on E. natalensis, D. rotundifolia and A. nilotica plants, spending up to three or four minutes on individuals of the first two species (Table 4.10.iii.). Only R. leptodictya was eaten for less than ten seconds on average. By far the longest duration of feeding in the late growing season was on V. rehmannii plants. G. flavescens plants were also favoured, one plant of this species was eaten by the goats for twelve minutes. Species eaten for less than 30 seconds included A. tortilis, B. africana, D. rotundifolia, R. leptodictya and P. africanum.

Despite the low feeding duration on R. leptodictya plants in the growing season, individuals of this species were fed on for an average of 140 seconds, and a maximum of ten minutes, in the early dry season. Other favoured plants at this time were the deciduous species C. molle, D. rotundifolia, and V. rehmannii. Only A. nilotica, O. pulchra, P. africanum and S. pungens were fed on for less than an average of 30 seconds. The species fed on for longest in the late dry season was E. natalensis. The goats spent up to eight minutes feeding on plants of this species. The leaves on the deciduous plants were sparse in the late dry season and the goats fed only for a brief period on such plants.

iv. Comparison between the Animal Species

The duration of feeding on individual woody plants was significantly correlated in the early growing season for the kudus and impalas, but there after no significant correlations were observed (Table 4.8).

The goats were the only animals to have a long feeding duration on E. natalensis; for D. rotundifolia the pattern was similar but less clearcut. For the kudus and impalas G. flavescens was a favoured food plant, but on average was eaten for slightly shorter periods by the goats. The impalas tended not to eat browse plants for long in the early growing season, but preferred to feed on grass.

V. rehmannii was favoured by all the animals in the late growing season. D. cinerea and G.flavescens plants were also eaten for longer duration than most other woody plant species. Although the former species was eaten by the goats for slightly shorter periods than by the kudus and impalas, and the latter was eaten slightly less by the impalas. The impalas spent more time feeding on the thorny Acacia plants than did the goats and especially the kudus. None of the animals ate D. rotundifolia.

V. rehmannii continued to be favoured by all the animals in the late dry season. The kudus and impalas also favoured A.

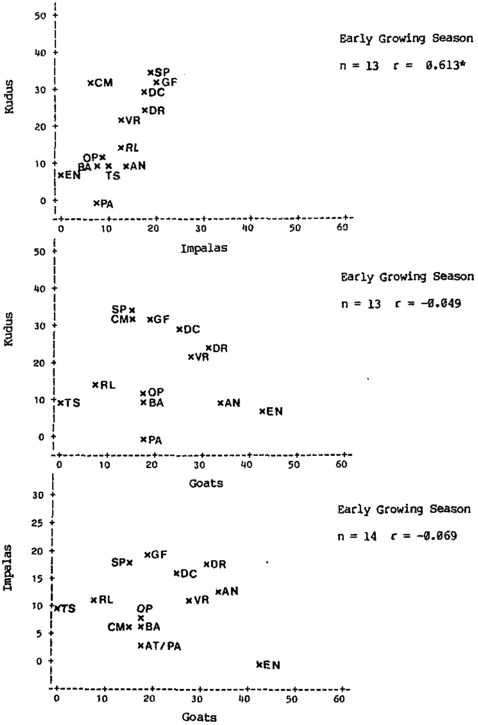


Fig 4.8. A Comparison of the Average Duration of Feeding on Individual Woody Plants by Kudus, Impalas and Goats.

i. *Early Growing Season.*

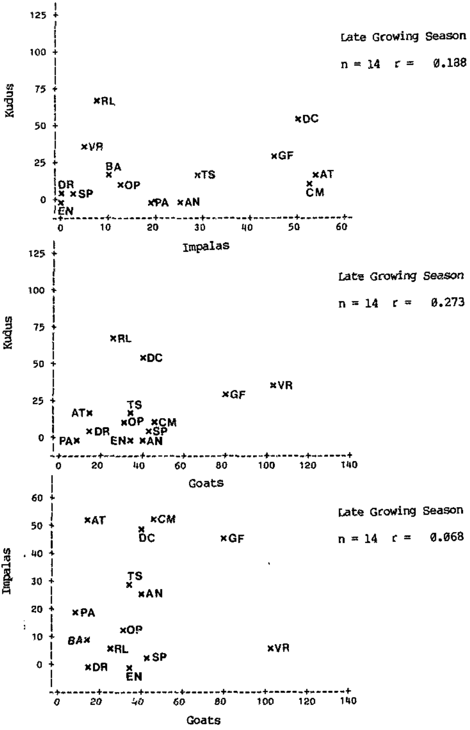


Fig 4.8. A Comparison of the Average Duration of Feeding on Individual Woody Plants by Kudus, Impalas and Goats.

ii. Late Growing Season.

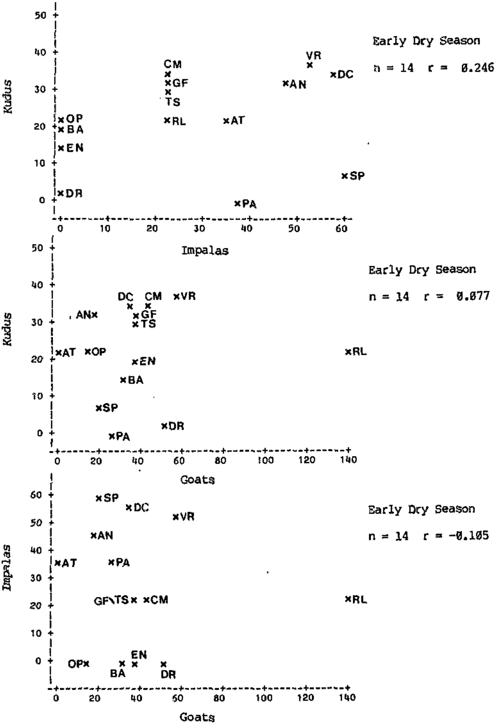


Fig 4.8. A Comparison of the Average Duration of Feeding on Individual Woody Plants by Kudus, Impalas and Goats. iii. Early Dry Season.

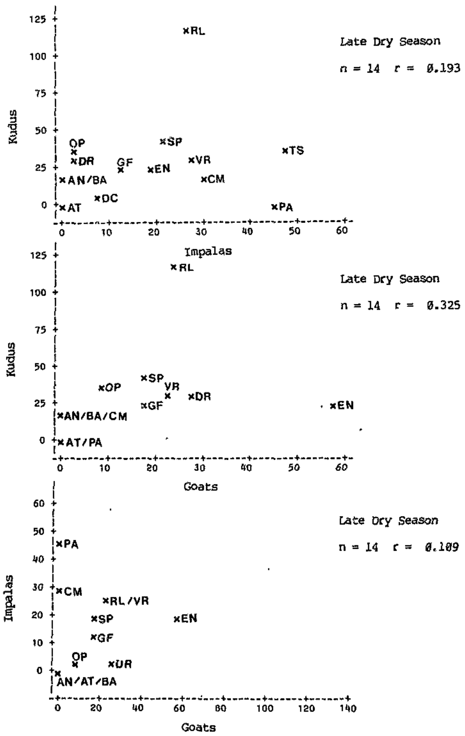


Fig 4.8. A Comparison of the Average Duration of Feeding on Individual Woody Plants by Kudus, Impalas and Goats.

iv. Late Dry Season.

nilotica and D. cinerea, the goats had a lower duration of feeding on these species. C. molle plants were eaten for longest by the impalas and goats. Neither B. africana nor O. pulchra were eaten in this season. The goats alone ate D. rotundifolia and had the highest feeding duration for R. leptodictya. The kudus fed for longer on G. flavescens and T. sericea plants than the other animal species did, but ate no P. africanum. The impalas alone favoured S. pungens.

In the late dry season the leaves were scarce on the deciduous plants. None of the animals fed for long on the microphyllous species. The goats had the longest feeding duration of E. natalensis and D. rotundifolia while the impalas favoured C. molle, T. sericea and P. africanum. The kudus had a long feeding duration on many woody plants in the late dry season but R. leptodictya and S. pungens were fed on for longest.

b. Common Forbs

The animals usually fed on an individual forb species for an average of less than a minute. Feeding durations on forbs are limited by the size of the plant except in the case of those species growing in large clumps.

i. Kudus

P. campestris and I. macra were the forbs eaten for longest by the kudus in the early growing season. The maximum time spent feeding on any one plant was 85 seconds for P. campestris (Table 4.11.i.). In the late growing season J. flava, W. indica and S. cordifolia were fed on for up to one minute, but generally less than half a minute.

J.flava and S. cordifolia continued to be favoured in the early dry season, along with P. campestris. Plants of J. flava and P. campestris wer eaten for up to two or three minutes. The three plants eaten for longest in the early dry season, plus W. indica, were the favoured species in the late dry season. These are all species with a clumped growth pattern. Species eaten for only a very short time throughout the year were E. alsinoides and O. herbacea, both of which grow in a dispersed pattern.

ii. Impalas

The impalas spent up to one minute feeding in J. flava patches in the early growing season, but the average feeding duration was a quarter of this time (Table 4.11.ii.). In the late dry season W. indica and P. campestris were favoured. The impalas spent up to five minutes feeding in W. indica patches.

The same species together with T. forbesii were eaten for longest in the early dry season. J. flava replaced T. forbesii in the late dry season. Again the longest times were spent feeding on W. indica. Plants not eaten for long by the impalas were E. alsinoides and O. herbacea.

Table 4.11. Duration of Feeding (seconds) on Individual Forb Plants.

i. Kudus

Species	Early Growing Season				Late Growing Season				Early Dry Season				Late Dry Season			
	Rank	Mean±SE	Max	n	Rank	Mean±SE	Max	n	Rank	Mean±SE	Max	n	Rank	Mean±SE	Max	n
Evolvulus alsinoides	-	0 ± -	0	0	-	0 ± -	0	0	-	0 ± -	0	0	-	0 ± -	0	0
Hermannia grisea	3	13 ± 2	36	15	4	13 ± 2	42	20	4	13 ± 2	28	20	6	8 ± 1	18	16
Indigofera macrantha	1	29 ±18	46	2	-	0 ± -	0	0	-	0 ± -	0	0	-	0 ± -	0	0
Justicia flava	6	10 ± 2	20	8	1	24 ± 4	81	41	1	27 ± 9	219	25	.	30 ± -	30	1
Oldenlandia herbacea	-	0 ± -	0	0	-	0 ± -	0	0	-	0 ± -	0	0	-	0 ± -	0	0
Pollichia campestris	2	17 ± 2	85	46	5	12 ± 2	32	23	2	18 ± 5	123	22	4	15 ± -	15	1
Sida cordifolia	7	9 ± 2	13	6	2.5	14 ± 4	59	17	3	17 ± 2	44	35	1	35 ±11	216	21
Solanum panduraeforme	4.5	12 ± 3	15	2	-	0 ± -	0	0	-	0 ± -	0	0	5	14 ± -	14	1
Tephrosia forbesii	-	0 ± -	0	0	-	0 ± -	0	0	6	11 ± 4	19	3	-	0 ± -	0	0
Waltheria indica	4.5	12 ± 3	53	17	2.5	14 ± 3	76	32	5	12 ± 1	29	59	3	20 ± 3	74	51

Table 4.11. Duration of Feeding (seconds) on Individual Forb Plants.

ii. Impalas

Species	Early Growing Season				Late Growing Season				Early Dry Season				Late Dry Season			
	Rank	Mean±SE	Max	n	Rank	Mean±SE	Max	n	Rank	Mean±SE	Max	n	Rank	Mean±SE	Max	n
Evolvulus alsinoides	7	3 ± 1	3	2	6	7 ± 1	7	2	–	0 ± –	0	0	–	0 ± –	0	0
Hermannia grisea	3	5 ± 1	10	13	–	0 ± –	0	0	5	16 ± 3	95	57	5	7 ± 2	20	13
Indigofera macrantha	–	0 ± –	0	0	5	9 ± 4	10	2	7	6 ± 3	11	3	–	0 ± –	0	0
Justicia flava	4	14 ± 5	70	12	–	0 ± –	0	0	–	0 ± –	0	0	1	51 ±33	84	2
Oldenlandia herbacea	–	0 ± –	0	0	–	0 ± –	0	0	–	0 ± –	0	0	–	0 ± –	0	0
Pollichia campestris	1	7 ± 1	21	22	2	28 ±21	174	8	2	24 ± 4	78	27	2	45 ± 7	51	2
Sida cordifolia	8	5 ± –	5	1	7	1 ± 0	1	2	6	13 ± 3	102	34	4	10 ± 2	34	27
Solanum panduraeforme	2	6 ± 1	18	14	3	13 ± 3	81	38	4	19 ± 6	110	20	–	0 ± –	0	0
Tephrosia forbesii	6	7 ± 1	11	3	4	10 ± 3	26	9	1	26 ± 7	124	24	–	0 ± –	0	0
Waltheria indica	5	6 ± 1	13	9	1	29 ±11	467	44	3	20 ± 2	205	212	3	23 ± 3	152	79

Table 4.11. Duration of feeding (seconds) on Individual Forb Plants.

iii. Goats

Species	Early Growing Season				Late Growing Season				Early Dry Season				Late Dry Season			
	Rank	Mean±SE	Max	n	Rank	Mean±SE	Max	n	Rank	Mean±SE	Max	n	Rank	Mean±SE	Max	n
Evolvulus alsinoides	4	11 ± 3	35	38	4	11 ± 4	30	10	7.5	4 ± -	4	1	-	0 ± -	0	0
Hermannia grisea	7	9 ± 1	62	88	6	5 ± 2	10	3	4	13 ± 2	190	85	3	12 ± 2	63	72
Indigofera macrantha	3	14 ± -	14	1	3	14 ± 4	44	12	9	1 ± -	1	1	-	0 ± -	0	0
Justicia flava	1	22 ± 6	49	8	-	0 ± -	0	0	1	32 ±13	132	9	1	23 ± 3	115	49
Oldenlandia herbacea	8	2 ± -	2	1	-	0 ± -	0	0	-	0 ± -	0	0	-	0 ± -	0	0
Pollichia campestris	2	15 ± 3	61	36	1	28 ± 7	96	16	2	26 ±13	141	10	3	12 ± 2	16	6
Sida cordifolia	5.5	10 ± 0	10	2	7	2 ± 0	2	1	6	10 ± 3	35	16	3	12 ± 2	70	44
Solanum panduraeforme	-	0 ± -	0	0	-	0 ± -	0	0	7.5	4 ± -	4	1	6	1 ± -	1	1
Tephrosia forbesii	-	0 ± -	0	0	2	20 ± 3	215	81	5	11 ± 7	18	2	-	0 ± -	0	0
Waltheria indica	5.5	10 ± 6	50	8	5	6 ± -	6	1	3	23 ± 2	230	109	5	11 ± 2	88	46

iii. Goats

The goats had the highest feeding duration on J. flava in the early growing season, but spent the maximum time on individual plants of P. campestris, W. indica and H. grisea (Table 4.11.iii.). In the late growing season the favoured plants were P. campestris and T. forbesii, with a maximum of three minutes being spent eating T. forbesii.

J. flava, P.campestris, W.indica and H. grisea were eaten for longest in the early dry season, up to four minutes being spent eating W. indica. In the late dry season J. flava was the favoured forb species. The plants O. herbacea and S. panduraeforme were least favoured by the goats throughout the year.

iv. Comparison between the Animal Species

In the early growing season plants of P. campestris were eaten for relatively long durations by all three animal species, but the patterns of feeding durations for the animals were not significantly correlated in the growing season (Fig 4.9.) J. flava plants were eaten for longest by the impalas and goats. Only the kudus favoured I. macra. The goats alone fed for long times on H. grisea and W. indica plants in this season.

By the late growing season all three animal species fed longest on P. campestris and J. flava plants. T. forbesii was of long feeding duration to the goats and W. indica to the impalas and kudus. Species eaten for only a few seconds, if at all in the growing season were E. alsinoides, O. herbacea and S. panduraeforme.

In the early dry season P. campestris continued to be favoured by all the animals. J. flava was favoured by both the kudus and goats. The feeding durations of these animals were significantly correlated at this time. The kudus also favoured S. cordifolia. W. indica was of long feeding duration to the impalas and goats but the impalas also favoured H. grisea. The goats alone favoured T. forbesii.

In the late dry season J. flava and W. indica were universally favoured. The impalas and goats also favoured P. campestris. There existed a significant correlation between the duration of feeding on forbs by these two animal species in the late dry season. The kudus differred in that they continued to favour S. cordifolia.

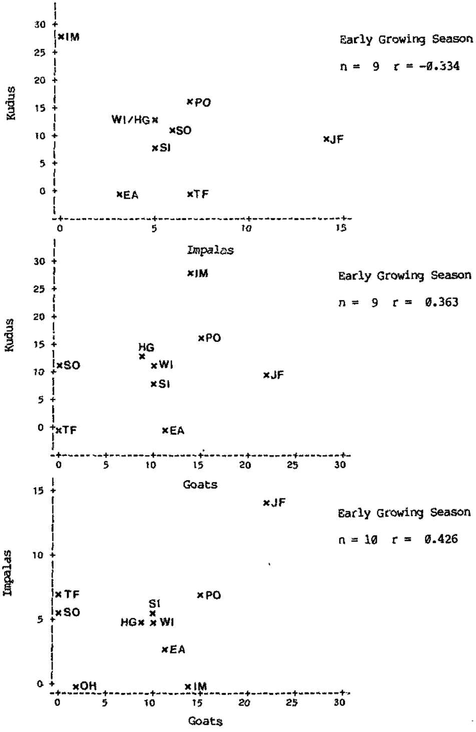


Fig 4.9. A Comparison of the Average Duration of Feeding on Forb Species by *Kudus*, Impalas and Goats.

i. *Early Growing Season.*

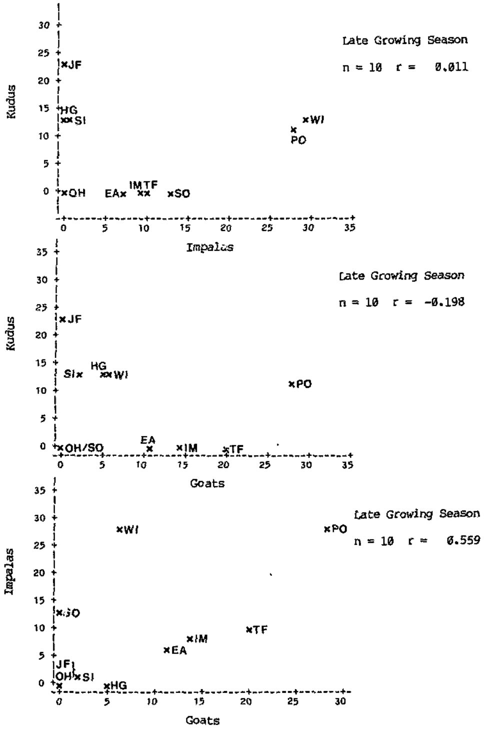


Fig 4.9. A Comparison of the Average Duration of Feeding on Forb Plants by Kudus, Impalas and Go[illegible].

ii. Late Growing Season.

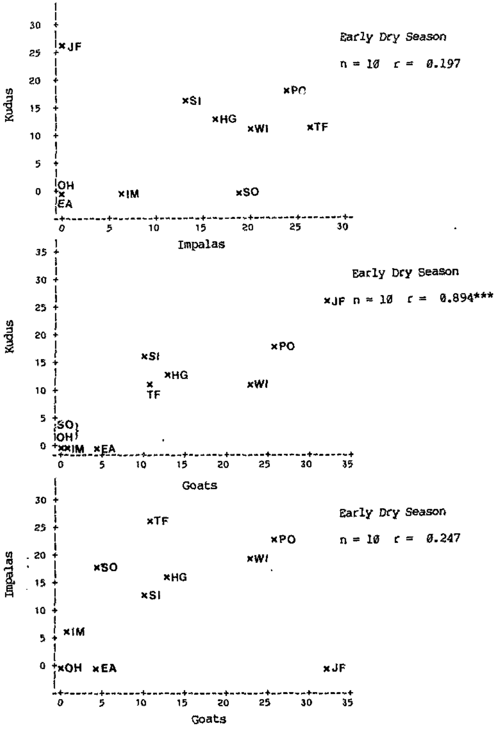


Fig 4.9. A Comparison of the Average Duration of Feeding on Forb Plants by Kudus, Impalas and Goats.

iii. Early Dry Season.

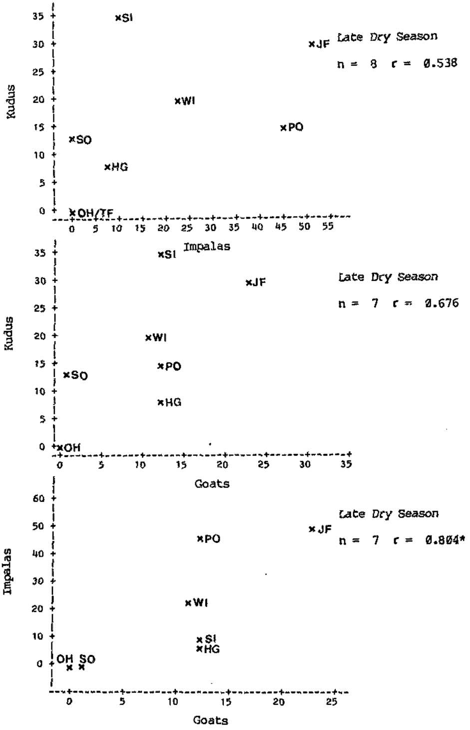


Fig 4.3. A Comparison of the Average Duration of Feeding on Forb Plants by Kudus, Impalas and Goats.

iv. Late Dry Season.

4.3.6. A Comparison of Techniques of Measuring Species Selection

a Common Woody Plants

i. Dietary Proportion and Acceptance Value

The dietary proportions and acceptance values of woody plants were correlated for the kudus during the growing season (Fig 4.10.). In the late growing season this relationship was mainly due to their high acceptance of the two principal dietary species G. flavescens and D. cinerea. The two measurements of species selection were not correlated for the kudus in the dry season. This was due to a high acceptance of the less common species V. rehmannii which did not account for a large proportion of the diet in the early dry season, and the converse trend for G. flavescens. In the late dry season many deciduous species were of high acceptance when they bore even a few leaves but contributed little to the diet. No correlation was observed between these two measurements for the impalas and goats in any season. In both cases this was due to a high acceptance for the Acacia species in the growing season and a high acceptance of the relatively less common R. leptodictya in the dry season. None of these plants accounted for a large part of the diet. Thus the proportional representation of a plant species in the diet of an animal was generally not representative of the animals preference, but is affected by the availability of food

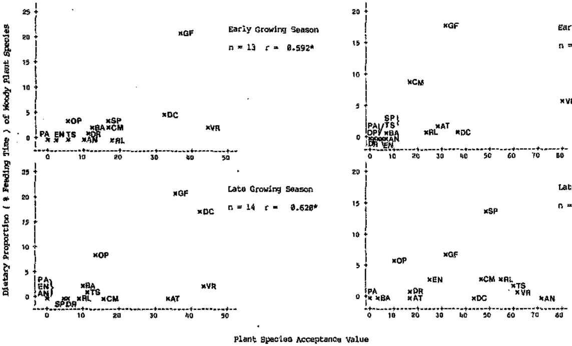


Fig 4.10. A Comparison between the Proportions of Woody Plant Species in the Diet of Browsing Ungulates and Measures of Preference.

I). Acceptance value

i. Kudus

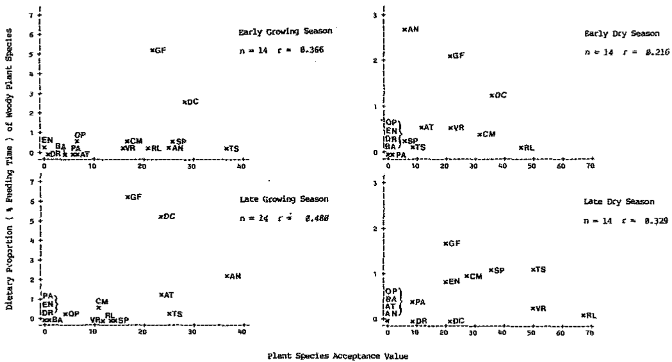


Fig 4.18. A Comparison between the Proportions of Woody Plant Species in the Diet of Browsing Ungulates and Measures of Preference.

i). Acceptance value

ii. Impalas

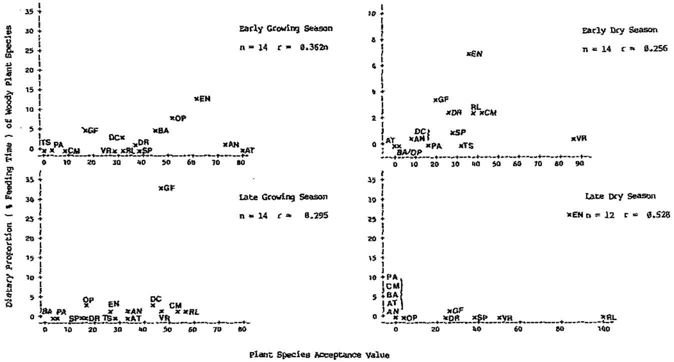


Fig 4.10. A Comparison between the Proportions of Woody Plant Species in the Diet of Browsing Ungulates and Measures of Preference.

i). Acceptance Value

iii. Goats

items.

ii. Dietary Proportion and Feeding Duration

The duration of feeding on woody plant species bore no relationship to the relative proportions of those species in the diet of the kudus (Fig 4.11.) This was due to a long duration of feeding on many species, including V. rehmannii and R. leptodictya, relative to their contribution to the diet. The disparity between these measurements was less for the impalas and a significant correlation developed in the late growing season when they fed for the longest average durations upon the two principal dietary species. For the goats the dietary proportion was correlated to the feeding duration in the late dry season and early growing season when these animals fed mainly on E. natalensis. But in the remaining two seasons a long feeding duration on V. rehmannii and R. leptodictya prevented a significant correlation developing between these two measurements. Hence the time an animal spends feeding on individual plants of a species is a poor indication of the quantitative importance of that species in the overall diet. The duration of feeding on a plant was a measure of preference rather than utilisation.

iii. Dietary Proportion and Selectivity Ratio

The selectivity ratio records the use of a plant species in relation to its abundance in the habitat. There was no correlation between the time spent feeding on plant species and the relative

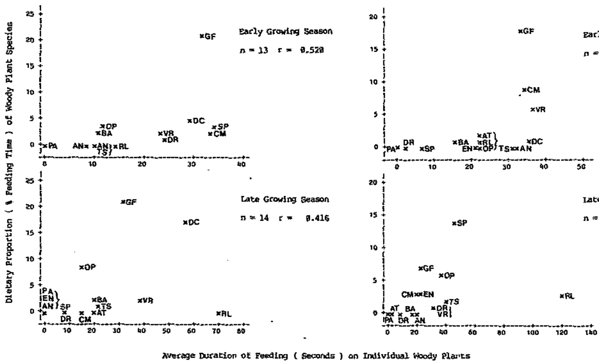


Fig 4.11. A Comparison between the Proportions of Woody Plant Species in the Diet of Browsing Ungulates and Measures of Preference.

ii). Feeding Duration

i. Kudus

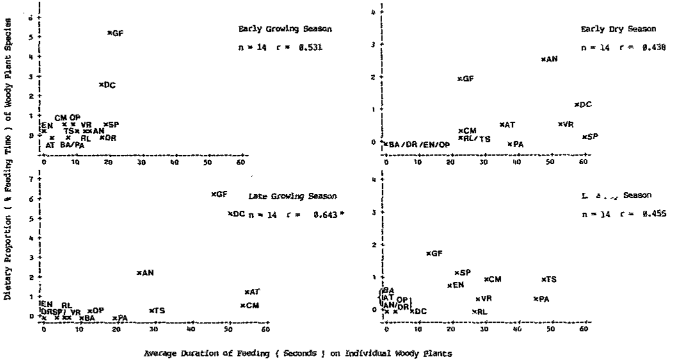


Fig 4.11. A Comparison between the Proportions of Woody Plant Species in the Diet of Browsing Ungulates and Measures of Preference.

ii). Feeding Duration

ii. Impalas

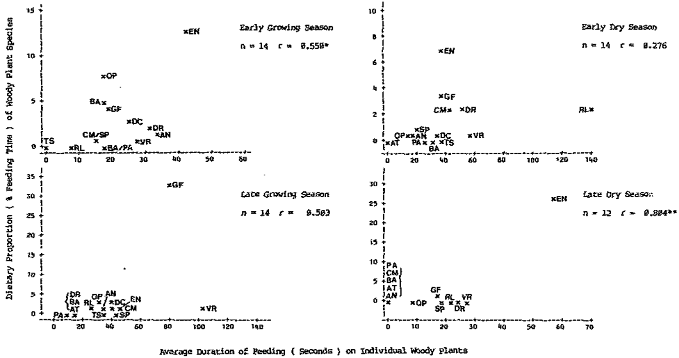


Fig 4.11. A Comparison between the Proportions of Woody Plant Species in the Diet of Browsing Ungulates and Measures of Preference.

ii). Feeding Duration

iii. Goats

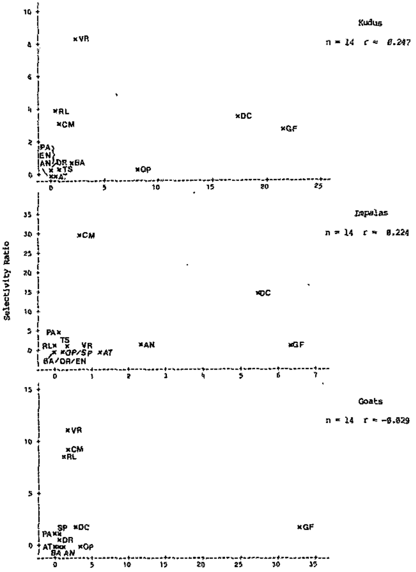
selection of species as measured by the selectivity ratio (Fig 4.12.). G. flavescens and for the kudus and impalas, D.cinerea, were of greater importance in the diet than indicated by the selectivity ratio, both are common species. For the kudus and goats, and to a lesser extent, the impalas the species C. molle, R. leptodictya and V. rehmannii were of high selectivity but low dietary proportion. Again the indication is that an animals preference is different to the dietary proportion which must be related to the relative availability of plant species.

iv. Dietary Proportion and the Abundance of Plant Species

Comparison with measures of preference indicated that the proportion of a plant species in the diet of the animal was influenced by the abundance of that species in the habitat. Overall the proportions of common woody plants in the diet of browsing ungulates were not correlated to the abundance of the species (Fig 4.13.). The animals spent only a short time feeding on several of the most abundant species such as O. pulchra, yet the time spent feeding on other species was disproportionately large. This indicates that although the relative use of plant species by the animals may be influenced by its abundance the animals are definitely selective in their choice of food items.

v. Acceptance Value and Feeding Duration

These two techniques both measure preference rather than utilisation of plant species. For the kudus the acceptance of



Dietary Proportion (% Feeding Time) of Woody Plant Species

Fig 4.12. A Comparison between the Proportions of Woody Plant Species in the Diet of Browsing Ungulates and Measures of Preference.

iii). Selectivity Ratio

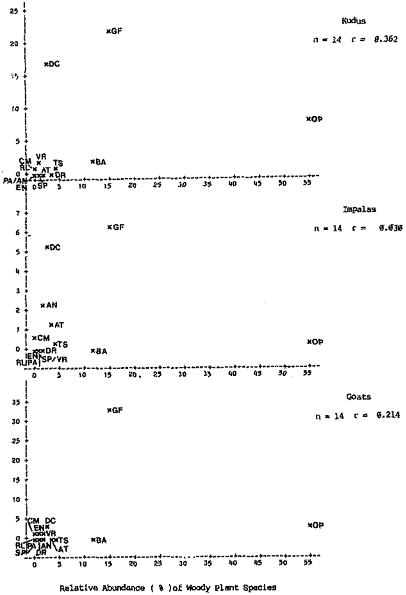


Fig 4.13. A Comparison between the Proportions of Woody Plant Species in the Diet of Browsing Ungulates and the Relative Availability of the Plants in the Habitat

woody plants was significantly correlated to the duration of feeding on individual plants in the growing and early dry seasons, while in the late dry season the duration of feeding on individual plants appeared to be restricted by the sparsity of leaves remaining on the deciduous species (Fig 4.14.). For the impalas and goats these measurements correlated only in the late growing and late dry seasons. A long duration of feeding on the few times that certain plants were eaten was the cause of the lack of correlation. The feeding patterns displayed by the two techniques for measuring preference gave more similar results than were obtained by measuring the proportions of woody plant species in the diet, however the correlations between acceptance and feeding duration were still not very strong.

vi. Acceptance Value and Selectivity Ratio

The acceptance of woody plant species was significantly correlated to the selectivity ratio for the kudus and goats but not for the impalas for which the acceptance values of T. sericea and the Acacia species were rather high (Fig 4.15.).

vii. Acceptance Value and Plant Species Abundance

No correlation occurred between the abundance of woody plant species in the late growing season and the acceptance values of these plants to kudus, impalas or goats, even when O. pulchra, which was of exceedingly high abundance and low acceptance, was removed from the comparison (Fig 4.16.). Thus the acceptance value

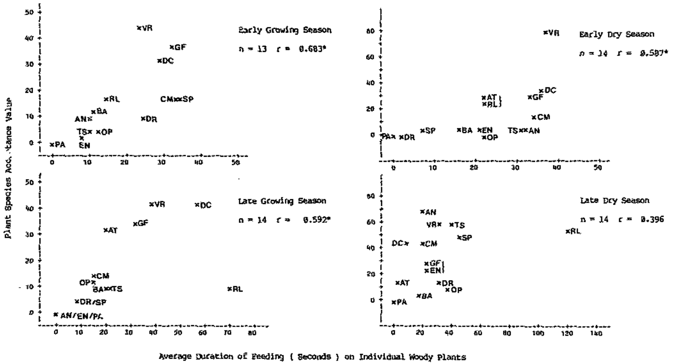


Fig 4.14. A Comparison of Preference Indices Obtained for Woody Plants using Different Techniques of Measurement.

i) Acceptance Value and Feeding Duration.

i. Kudus

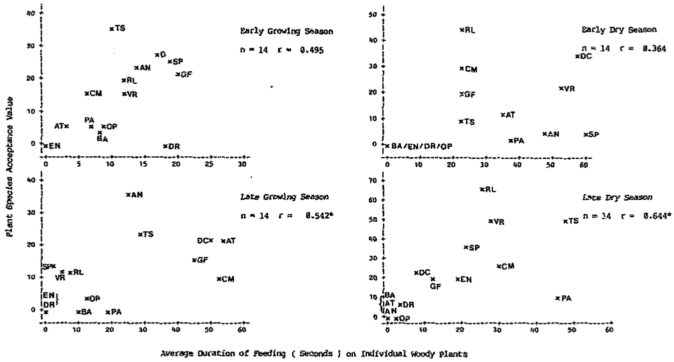


Fig 4.14. A Comparison of Preference Indices Obtained for Woody Plants using Different Techniques of Measurement.

i) Acceptance Value and Feeding Duration.

ii. Impalas

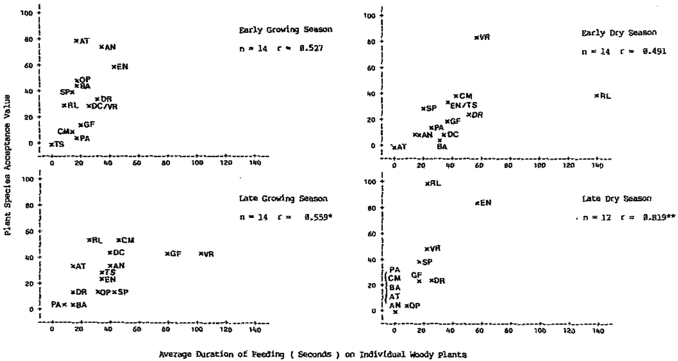


Fig 4.14. A Comparison of Preference Indices Obtained for Woody Plants using Different Techniques of Measurement.

i) Acceptance Value and Feeding Duration.

iii. Goats

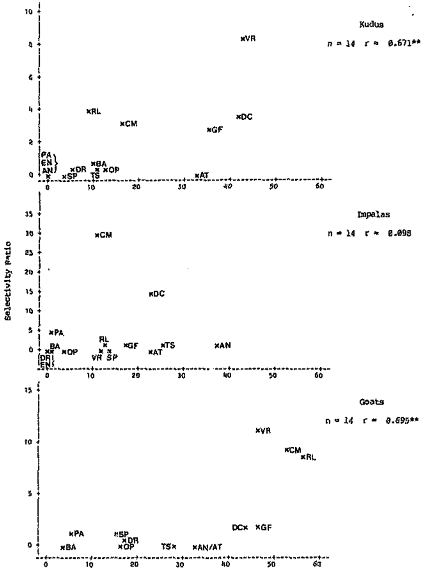


Fig 4.15. A Comparison of Preference Indices Obtained for Woody Plants using Different Techniques of Measurement.

ii) Acceptance Value and Selectivity Ratio.

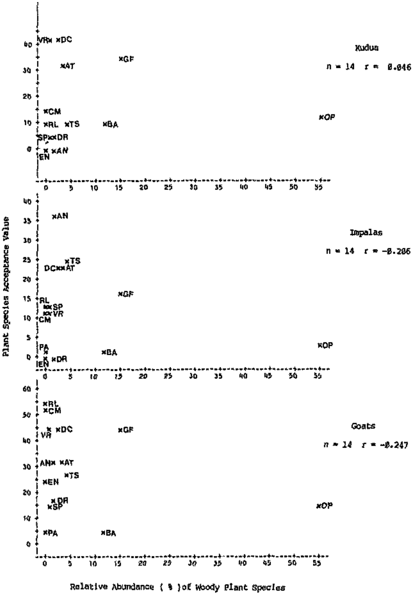


Fig 4.16. A Comparison between the Acceptance Values of Woody Plants in the Late Growing Season and the Relative Availability of Plants in the Habitat

of a plant species appears to be fairly independent of the relative abundance of that species in the habitat.

viii. Feeding Duration and Selectivity Ratio

For all three animal species the duration of feeding on a plant once encountered was significantly correlated to the selectivity ratio in the late growing season (Table 4.17.). Both these techniques are a measure of the animals preference and thus should be expected to correlate.

b. Common Forbs

i. Dietary Proportions and Acceptance Value

In contrast to the woody plants the proportions of forb species in the diet of the animals was often similar to the acceptance patterns. These two measurements were correlated in all seasons for the kudus (Fig 4.18.). For the impalas and goats a low acceptance of W. indica spoilt the correlation in the mid-year but the correlations were significant in the early growing season and late dry season. Thus it may be that the animals tend to eat forbs as they are encountered rather than selecting between many different species many of which which have a low rate of encounter.

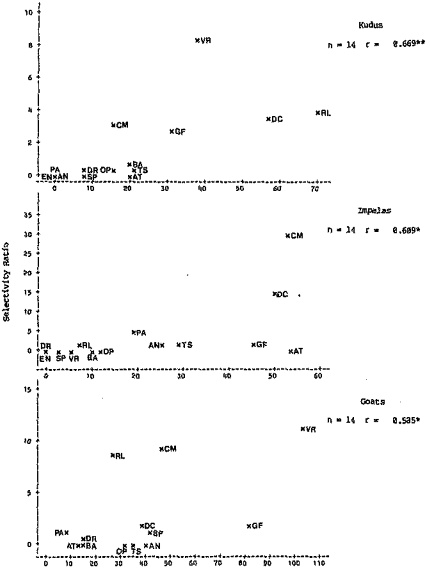


Fig 4.17. A comparison of Preference Indices Obtained for Woody Plants using Different Techniques of Measurement.

iii) Feeding Duration and Selectivity Ratio.

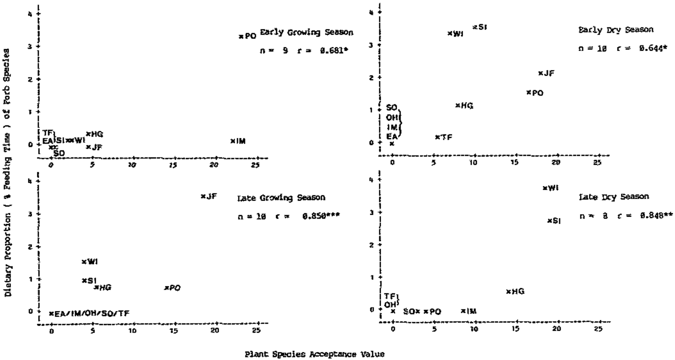


Fig 4.18. A Comparison between the Proportions of Forb Species in the Diet of Browsing Ungulates and Measures of Preference.

i). Acceptance value

i. Kudus

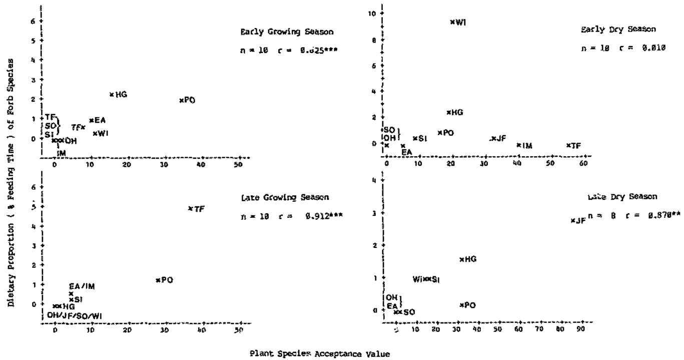


Fig 4.18. A Comparison between the Proportions of Forb Species in the Diet of Browsing Ungulates and Measures of Preference.

i). Acceptance value

ii. Impalas

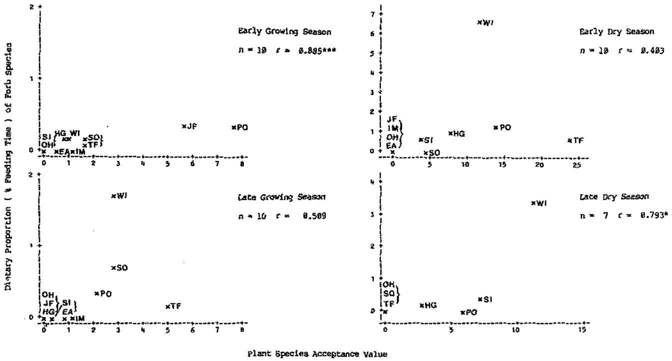


Fig 4.18. A Comparison between the Proportions of Forb Species in the Diet of Browsing Ungulates and Measures of Preference.

i). Acceptance value

iii. Goats

ii. Dietary Proportions and Feeding Duration

The dietary proportions were less similar to the feeding durations than to the acceptance values. The feeding duration was positively correlated to the dietary proportions for impalas in the growing season and for the kudus in the late growing and early dry seasons (Fig 4.19.). For the goats similatities existed in the late growing season, when P. campestris and T. forbesii dominated the feeding, and again in the late dry season. The duration of feeding on forbs is likely to be limited by the size of the plants, unless they are of clumped growth pattern. In most cases where these two measurements were not correlated this was due to a long duration of feeding on the P. campestris and J. flava, both of which tend to grow in a clumped pattern in the shade of trees.

iii. Acceptance Value and Feeding Duration

These two measures of preference gave similar results, particularly for the kudus and impalas, for which strong correlations were observed (Table 4.20.) The acceptance and feeding duration were positively correlated for the goats in the late growing and late dry seasons, but in the remaining seasons a long duration of feeding on several clumped species of low to intermediate acceptance prevented the occurrence of a significant correlation. However it does seem that as for woody plants these two measures of preference do give broadly similar results.

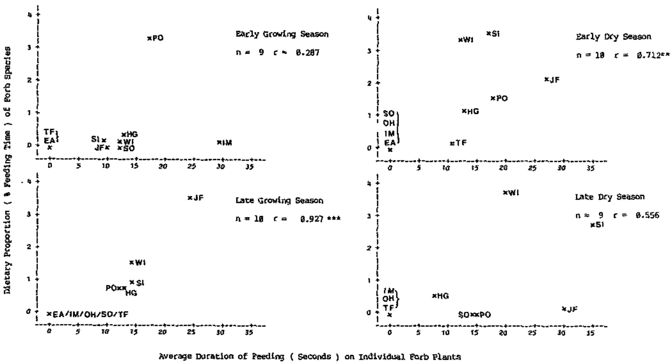


Fig 4.19. A Comparison between the Proportions of Forb Species in the Diet of Browsing Ungulates and Measures of Preference.

ii). Feeding Duration

i. Kudus

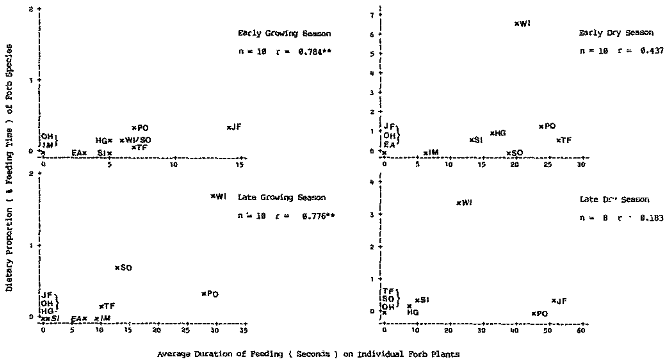


Fig 4.19. A Comparison between the Proportions of Forb Species in the Diet of Browsing Ungulates and Measures of Preference.

ii). Feeding Duration

ii. Impalas

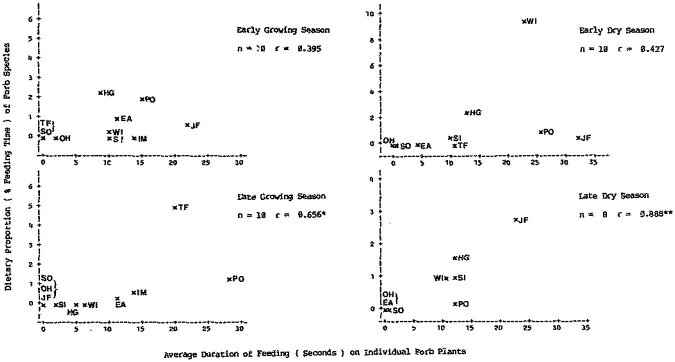


Fig 4.19. A Comparison between the Proportions of Forb Species in the Diet of Browsing Ungulates and Measures of Preference.

ii). Feeding Duration

iii. Goats

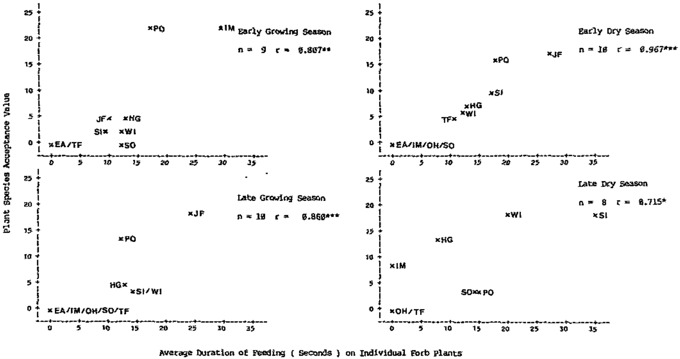


Fig 4.20. A Comparison of Preference Indices Obtained for Forb Species using Different Techniques of Measurement.

1) Acceptance Value and Feeding Duration.

i. Kudus

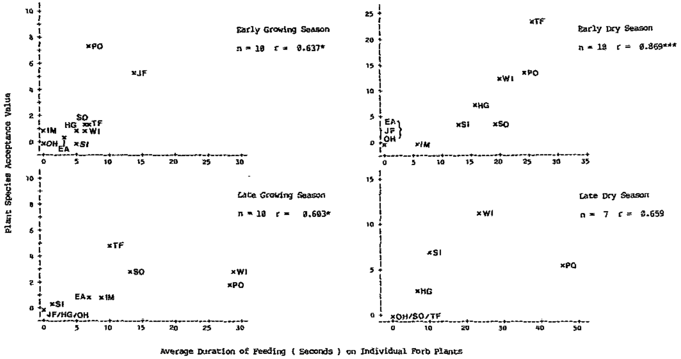


Fig 4.20. A Comparison of Preference Indices Obtained for Forb Species using Different Techniques of Measurement.

i) Acceptance Value and Feeding Duration.

ii. Impalas

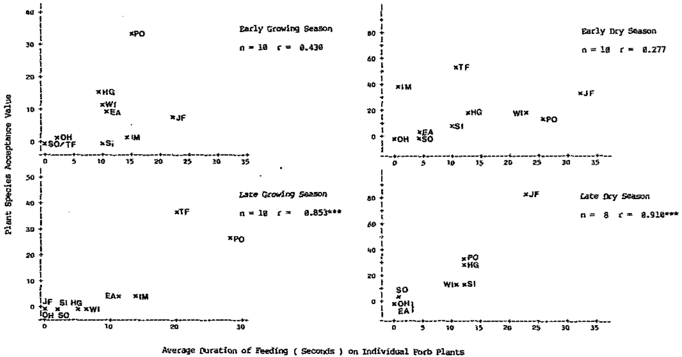


Fig 4.20. A Comparison of Preference Indices Obtained for Forb Species using Different Techniques of Measurement.

i) Acceptance Value and Feeding Duration.

iii. Goats

4.4. DISCUSSION

1. Dietary Selection by Browsing Ungulates

Ruminants can be classified into two main feeding types: browsers (concentrate selectors) and grazers (bulk and roughage feeders) according to the stomach structure (Hofmann & Stewart 1972, Hofmann 1973). Kudus fall into the category of browsers, while impalas and goats form an intermediate group referred to as mixed-feeders. These animals have the basic large rumen capacity of the grazer but with the increased papillation of the browser. For impala at least the extent of papillation can vary according to the diet being taken.

The diet of the tame kudus observed at Nylsvley comprised mainly woody browse. This is in agreement with previous studies on wild kudu (Wilson 1965, 1970, Owen-Smith 1979, Novellie 1983). Most of the browse was eaten directly from the plants. Fallen leaves of woody plants were not important in the dry season diet of kudus as they were for the goats and impalas, and are not mentioned as being important in the literature. Forbs occupied only 10 to 20% of the feeding time of the kudus at Nylsvley, but in the <u>Acacia nigrescens</u> savanna of the Kruger National Park kudus spent over half their time feeding in the herbaceous layer during the wet season (Novellie 1983).

Kudus are rarely reported as eating significant quantities of grass. One record of a kudu culled on the margin of a vlei in Wankie, National Park, Zimbabwe, showed the stomach to contain 80% grass, but other kudus culled from the same park contained less than 15% grass (Conybeare 1975). In the Kruger National Park the rumens of culled kudus contained only 5-10% grass (Giesecke and van Gylswyk 1975). They did, however, eat the new grass available on the burned areas (Owen-Smith 1979, Novellie 1983). The proportion of grass in the diet varies with the vegetation type. Rumens of kudus shot in the Kyle National Park, Zimbabwe, contained 30% grass in the Brachystegia / Julbernardia woodlands, 18% grass in Combretum / grass savannas and only 3% in Acacia savannas (Wilson 1970).

Fruit was sought out in the dry season. When the S. caffra trees were fruiting the kudus walked directly from tree to tree eating the fallen fruits. Other fruits eaten in the dry season were Acacia pods, and the tiny berries of G. flavescens. Fruits of the Strychnos species were eaten at all times of year.

The impalas at Nylsvley were preferential grazers of green grass. They spent significantly more time grazing than the kudus throughout the year, and they ate more grass than the goats in the early growing season. In the dry season green grass was scarce and the impalas turned to browse as an alternative source of food, but as soon as the first flush of new grass appeared on the burned firebreaks the impalas congregated on these areas feeding almost exclusively on the new grass which preceded the emergence of new leaves on the majority of woody plant species. Other studies confirm the classification of impalas as preferential grazers capable of using browse material. Typically the diet contains 45-[illegible] grass (Talbot and Talbot 1962, Van Zyl 1965, Jarman 1971, McAllister and Bornman 1972, Monro 1979, Dunham 1980), but can range from 5% (Jarman 1971), to over 90% in areas where browse is sparse [illegible]mprey 1963, Stewart 1971). The impalas both in this study and at Sengwa, Zimbabwe, increased their consumption of grass a few days after rainfall, presumably due to a new flush of green grass (Dunham 1980), or the "resurrection" or greening of dried grasses (Goldring pers. comm.).

The impalas ate far less browse than the kudus and goats. Trees and shrubs were browsed by impala mainly during the wet season. The total proportion of woody plant foliage in the diet increased in the dry season as fallen leaves from palatable trees were eaten. Impalas in the Sengwa Wildlife Area, Zimbabwe, also rely heavily on fallen leaves to see them through the dry season (Dunham 1980).

Like the kudus the impalas actively sought out fruit, walking directly from one fruiting tree to another in search of fallen fruit. Fruit production in savannas is erratic (Rutherford 1982). In the second year of the study there was a heavy crop of Acacia pods. The impalas ate these pods rather than leaf litter and forbs as in the previous dry season. The importance of these seedpods to wildlife has long been recognised (Burtt 1929, Stevenson & Hamilton 1947, Brooks 1961, Lamprey 1963, Dougall et. al. 1964). Acacia pods are also favoured by domestic livestock and may form up to 65% of the dry weight intake of cattle (Gwynne 1969). Heavy use of Acacia pods by impalas at Nylsvley in June and July has been recorded previously by Monro (1979) for his tame, penned impala. There were noticeably more Acacia pods lying on the ground inside the enclosure than just outside, so the high proportion of pods in the diet of the tame impalas may be as a consequence of less competition for this food resource inside the enclosure as compared to outside.

In Sengwa, Zimbabwe, forbs were a much more important dietary component for impalas than at Nylsvley, being the principal food in the late growing and early dry seasons (Dunham 1980). This may be due to a difference in the availability of forbs. Dunham (1980) found that the browse to graze ratio of the diet was determined by the browse to graze ratio in the vegetation.

The goats ate more grass in the growing season than the kudus did. On a year round basis grass formed less than half the diet of the goats in this study. This is generally true of goats (Edwards 1948, Du Toit 1972), unless browse is unavailable or the grass particularly attractive (Knight 1965, Du Toit 1972, Aucamp 1976, Nge'the and Box 1976, Field 1978). Woody browse was particularly heavily utilised in the early growing season and late dry season. Increased use of woody plants in the dry season was also observed for goats in Kenya (Field 1978). Fallen leaves, in particular those of Z. mucronata and S. cocculoides were a very important source of food for the goats in the dry season. This use of fallen leaves was also documented by Edwards (1948), while the winter diet of goats in Kenya contained only 5% fallen leaves (Field 1978). This is a much smaller proportion than at Nylsvley but the abundance of woody plants was not reported. The goats began to eat large quantities of leaf litter two months before the impalas, presumably due to depletion of the preferred food resources within their small home range. The goats, like the impalas, ate forbs mainly in the early dry season. The goats studied by Knight (1965) ate similar proportions of forbs to the animals at Nylsvley.

Fruit, in particular Acacia pods, were sought by the goats. These pods are good quality winter forage (Gwynne 1969), so much so that goatherds in Kenya claim individual ownership of fruiting Acacia tortilis trees in order to feed their livestock (Edwards 1948). Other fruits eaten were G. flavescens berries, Combretum seed pods and broken pieces of the large fruits of Strychnos species.

2. Dietary Proportions

i. Woody Plants.

The relative proportions of woody plant species in the diet of the three different animal species were correlated in the peak growing season when food is plentiful. This suggests a similar basis for their food choice. However, the time spent browsing by impalas in particular is much less than that of the kudus or goats. The wide overlap in the utilisation of browse species by ungulates has been recorded in other studies (Kelso unpublished, Grunow 1980).

Plant families and subfamilies generally favoured by browsing ungulates in this study were the Mimosoideae, Verbenaceae, Boraginaceae, and to a lesser extent the Combretaceae. Members of the Caesalpinioideae and Ochnaceae were not favoured. Other families like the Tiliaceae contained both favoured and non-preferred species.

Naturally the abundant species tend to predominate in the diet provided they are reasonably palatable. Two common species, G. flavescens and D. cinerea, were the principal food species at Nylsvley. A dependence on a few principal browse species in the growing season has been indicated in previous studies. Acacia, Combretum, Grewia and Ziziphus species are frequently the major food plants.

In this study the Acacia species were often eaten by the impalas, but were not principal food species since less than 10% of the study area was comprised of Acacia veld. Acacia species were the principal food plants for impalas in the Serengeti (Jarman & Gwynne, unpublished), and for goats in Kenya (Knight 1965, Nge'the & Box 1976, Field 1978). The large leaved Acacia caffra dominated the diets of both kudu and eland in Pilanesberg Game Reserve in Bophuthatswana (Kelso unpublished).

Combretum species are also generally favoured. They tend to retain their leaves longer than most other deciduous trees and so are important sources of food to browsers in the early dry season (Kerr et. al. 1970, Hall-Martin 1974, Novellie 1983). In the

Kruger National Park Acacia nigrescens together with Combretum apiculatum and Combretum heteroense formed 28% of the dry season diet of kudus (Novellie 1983). The first two species also comprised 48% of the rumen contents of giraffe in the nearby Timbavati Reserve (Hall-Martin 1974). For impalas at Sengwa, Zimbabwe, Combretum mossambicense was the principal browse species (Dunham 1980).

Grewia flavescens was the major food plant for all three animal species studied at Nylsvley. Grewia species are also important in other areas. More than 50% of the feeding time of giraffe in the Serengeti was comprised of Acacia tortilis and Grewia species in the wet season (Pellew 1982). In the lowveld of Zimbabwe the major food species for eland are Combretum apiculatum and Grewia species (Kerr et. al. 1970), while in the Waterberg, Namibia, Terminalia sericea replaces Combretum in the diet of eland and Grewia species are also important (Jankowitz 1982).

Although Ziziphus mucronata was rare at Nylsvley it was the principal food resource of kudus in the Umfolozi Game Reserve in Natal (O'Regan unpublished). Ziziphus abyssinica and Acacia senegal together made up 56% of the feeding time of giraffe in the Kidepo Valley, Uganda in the wet season (Field & Ross 1976).

Dichrostachys cinerea was a principal food plant of the indigenous animals at Nylsvley where it is common. It is structurally defended by spines, similar to the thorny Acacia and

Ziziphus species which are important food plants in other areas (Knight 1965, Field & Ross 1976, Field 1978, Novellie 1983, Kelso unpubl. O'Regan unpubl.).

Evergreen species only made up a significant proportion of the diet of the animals at Nylsvley in the late dry season. Other browsers such as gerenuk, also eat evergreens increasingly throughout the dry season (Leuthold 1970), and these plants are important for the winter survival of the lesser kudu in Tsavo National Park, Kenya (Leuthold 1971). At Nylsvley S. pungens foliage formed a large proportion of the winter diet of the impalas and kudus but less important to the goats, because the greatest density of S. pungens bushes was in eastern side of the enclosure, far from the home range of the goats. Instead the goats utilised E. natalensis. The less common E. undulata was also a dry season food species. The Euclea species are generally eaten only in the dry season. E. undulata, together with Colophospermum mopane and Albizia harveyi are important winter foods to giraffe in Timbavati (Hall-Marrin 1974), and eland in Zimbabwe utilise Euclea divinorum (Kerr et. al. 1970).

Several common species are only eaten when in new leaf and are ignored once the leaves mature, O. pulchra was particularly favoured by the kudus and goats at this time as it was one of the first species to produce new leaves. The impalas ate less of these new woody plant leaves preferring to feed mainly on the grass emerging on areas which had been burned in the dry season.

P. africanum was the least used of the common woody species at Nylsvley. The impalas and goats nibbled the leaves in the late dry season but the kudus were never seen to eat this species. However P. africanum is reported to be a principal food plant of giraffe in the western Transvaal (Sauer et. al. 1977). This however appears to be an effect of availability. Dichapetalum cymosum is a common woody geophyte in the Burkea savanna. This plant produces tempting new green leaves at the end of the dry season, when the availability of browse for the animals is at a minimum. These leaves contain monofluoroacetate, a highly toxic heart poison .. vertebrates. The kudus and impalas were never seen to eat this plant, but the domestic goats tried to eat the new leaves and one died as a consequence. The older less poisonous leaves were not seen to be eaten by the goats when alternative food was more plentiful.

The goats utilised a wider range of less common woody plant species than the other animals maybe as a consequence of their depleting the favoured food species in their small home range. Rare species were generally not all favoured by the animals but showed a range of acceptances.

The leaves eaten mainly as leaf litter by the impalas and goats come from three main species. The ubiquitous T. sericea, which is also used mainly in the dry season by the kudus, and S. cocculoides and Z. mucronata, most individuals of which exist mainly as tall trees out of reach of the browsers. Z. mucronata is a highly preferred food plant in areas where it is abundant

(O'Reagan unpublished). Eland, like impala are mixed grazer-browsers and in the Waterberg, Namibia, leaf litter was an important source of food to these animals in the dry season, in particular the leaves of T. sericea and Z. mucronata (Jankowitz 1982).

Generally the plants of a genus are similar in their patterns of utilisation by browsers. The similarities in the chemical structure... plant species have been used in plant taxonomy (Hegnau... ...bbs 1974), but it cannot be presumed that all plants with... genus are edible as chemical variation and polymorphism are well documented (Cates & Rhoades 1977, Cooper-Driver et. al. 1977, Chew & Rodman 1979). The Grewia species show a variety of patterns of acceptance by browsers, indicative of inter specific variation in the plant defence compounds. G. flavescens is a principal food species as are many other Grewia species (Kerr et. al. 1970, Hall-Martin 1974, Jankowitz 1982), yet Grewia monticola is only eaten occasionally, mainly in the dry season, and Grewia bicolor and Grewia flava are generally unpalatable, only being eaten only occasionally in the early growing season.

ii. Forbs

The relative utilisation of forbs by the three animal species was only similar for a few species. Plant families generally favoured were the Amaranthaceae, and Acanthaceae, while forbs of the Cucurbitaceae and Asclepiaceae were rarely eaten.

The diversity of forb species was high and as a consequence the encounter rate of the animals with the less common forb species was very low. The species composition and abundance of forbs appears to depend upon the pattern of rainfall. 1982 was drier than the previous year, with the rainfall occurring late in the year. Three species of forbs which had previously been common were not abundant in the following year and were replaced by species which were previously of less importance.

Many species of forbs were eaten in small quantities. This could be to avoid the ingestion of significant amounts of any deleterious plant substances (Freeland & Janzen 1974). The indigenous animals were not seen to eat the forbs known to be highly toxic, including the Kalanchoe and Asclepias species (Watt & Breyer-Brandwijk 1962), but these species were eaten occasionally by the goats even in the late growing season when there was plenty of alternative food available.

3. Measuring Preference

In order to identify the factors controlling the consumption of browse plants by large herbivores it is necessary to determine the relative preferences exhibited by the animals for each plant species. The magnitude of the preference should be meaningful and the differences in preference values both between and within species statistically proven. Techniques merely giving a rank order of preference are inadequate for the purpose of this study, as it is required that the measure of preference be related to quantitative measures of chemical factors within the plants.

The time spent feeding on a species is a measure of dietary contribution not preference, and is greatly influenced by the availability of potential food species. Highly preferred but rare species can only make up a small portion of the diet, while common but less preferred species can make a larger contribution to the diet (Petrides 1975).

Preference is not a static measurement but may vary greatly, both on a daily and a seasonal basis (Arnold & Dudzinski 1978). The preference for a plant may depend on the availability of other more highly preferred plants (Atsatt & O'Dowd 1976, Pyke et. al. 1977, McNaughton 1978), the state of hunger of the animal (Goatcher & Church 1970, Pulliam 1974) and individual variation within both the plants (Hughes 1979, Bryant & Kuropat 1980), and the herbivores (Arnold & Dudzinski 1978, Willms & McLean 1978).

The forage or selectivity ratio is the most common method of calculating preference. This method compares the degree of utilisation of a plant species in relation to its abundance in the habitat. Plants that are more common in the diet than in the habitat are said to be preferred (Petrides 1975, Pyke et. al. 1977, Lechowitz 1982). However whether a species is classified as preferred or not depends on what was viewed as being available (Strauss 1979, Johnson 1980, Loehle & Rittenhouse 1982). In this study had grass been included in the calculations the results would have been very different, especially for the impalas which eat much grass. Hence this technique was not chosen to demonstrate the patterns of preference of the herbivores.

The acceptance value of a plant species is a measure of the frequency with which it is eaten when encountered. This solves much of the problem of estimating what is available to the animals, as only the plants within reach of the animals mouth are recorded as being available and no assumptions of the animals ability to detect plants, or of their patterns of movement within the habitat are imposed on the data. The acceptance values obtained for each species are amenable to statistical comparison between species and seasons. Plants can be grouped into fairly discrete categories according to their patterns of acceptance to the animals (Tables 4.12. & 4.13). These groups are i.) favoured species of high acceptance to the animals when in leaf, most of these species being deciduous, ii.) intermediate species which are eaten throughout the year but at lower acceptance values, and iii.) non-preferred species which are rarely eaten if at all, within the latter two groups are a.) the dry season reserve species which are eaten increasingly in the dry season as the availability of the favoured plants declines, and secondly b.) the temporary species which are eaten only when in a specific phenological phase, usually as immature leaves. The acceptance value, like most measures of preference,is is influenced by very small sample size. Another draw back is that this measure takes no account of the fact that once an animal has begun to eat a plant it may feed extensively or just nibble a few leaves.

Table 4.12. Classification of Woody Plant Species According to the Patterns of Acceptance to Browsing Ungulates.

Classification	Kudus	Impalas	Goats
Principal	Grewia flavescens	Grewia flavescens	Grewia flavescens
Species	Dichrostachys cinerea	Dichrostachys cinerea	
Favoured	Combretum zeyheri	Acacia nilotica	Euclea natalensis
Species	Ehretia rigida	*Ehretia rigida*	Grewia monticola
		Erythrococca menyharthii	Ozoroa paniculosa
		Terminalia sericea	Rhus leptodictya
	Vitex rehmannii		Vitex rehmannii
Intermediate	Acacia karoo	Acacia karoo	Acacia karoo
Species	Acacia nilotica		Acacia nilotica
	Acacia tortilis	Acacia tortilis	Acacia tortilis
	Erythrococca menyharthii		Erythrococca menyharthii
	Strychnos cocculoides	Strychnos cocculoides	Strychnos cocculoides
	Diospyros lycioides		*Grewia bicolor*
	Securidaca longipedunculata	Securidaca longipedunculata	Securidaca longipedunculata
			Terminalia sericea
Intermediate		Carissa bispinosa	Carissa bispinosa
but increasing	Combretum molle	Combretum molle	*Combretum molle*
in the Dry	Rhus leptodictya	Rhus leptodictya	Dombeya rotundifolia
Season	Strychnos pungens	Strychnos pungens	Strychnos pungens
	Terminalia sericea	Securidaca longipedunculata	Grewia flava
	Ziziphus mucronata	Ziziphus mucronata	Ziziphus mucronata
		Vitex rehmannii	*Euclea natalensis*
		Euclea undulata	Euclea undulata
Dry Season	*Carissa bispinosa*	Diospyros lycioides	Diospyros lycioides
Reserve	Euclea natalensis	Euclea natalensis	
Species	Euclea undulata		
	Grewia monticola		

Table 4.12. Continued. . .

Temporary		Acacia burkei	Acacia burkei
Species	Burkea africana		*Burkea africana*
eaten only as	*Dombeya rotundifolia*	Lannea discolor	Lannea discolor
new leaves	Ochna pulchra	Ochna pulchra	
Rejected or	Dichapetalum cymosum	*Dichapetalum cymosum*	Dichapetalum cymosum
rarely eaten	Peltophorum africanum	Peltophorum africanum	Peltophorum africanum
Species	Acacia burkei	Burkea africana	
	Lannea discolor	Dombeya rotundifolia	
	Grewia bicolor	Grewia bicolor	
	Grewia flava	Grewia flava	
		Grewia monticola	
		Ochna pulchra	

Table 4.13. Classification of Forb Species According to the Pattern of Acceptance to Browsing Ungulates.

Classification	Kudus	Impalas	Goats
Favoured	Pollichia campestris	*Pollichia campestris*	Pollichia campestris
Species	Justicia flava	Tephrosia forbesii	Tephrosia forbesii
	Justicia minima		Pentarrhinum insipidum
	Justicia *spergulaefolia*		
	Lippea javanica		
Intermediate	*Achyropsis* leptostachya		Achyropsis leptostachya
Species	Asparagus buchananii		Asparagus suaveolens
	Becium angustifolium	Becium angustifolium	
	Cassia capensis		Cassia capensis
	Bauhinia macrantha	Evolvulus alsinoides	
	Commelina ecklonlana	Felicia fascicularis	
	Commelina erecta		
	Elephantorrhiza obliqua		
	Hermbstaedtia odorata	Polygala *sphenoptera*	
	Indigofera comosa	Plumbago zeylanica	Indigofera distincta
	Indigofera macra	Indigofera macra	Indigofera macra
	Justicia incerta	*Justicia incerta*	
	Pavonia transvaalensis	Pterococcus africana	Pterococcus africana
	Senecio venosus	Solanum panduraeforme	Senecio inaequidens
	Triumfetta pentandra		Rhynchosia confusa
Intermediate	Hermannia grisea		Hermannia grisea
but *increasing*		Justicia minima	Justicia flava
in the Dry		Lippea javanica	
Season	Sida cordifolia	Sida cordifolia	
	Waltheria indica	Waltheria indica	Waltheria indica
Dry Season	Achyranthes sicula	Achyranthes *sicula*	Achyranthes sicula
Reserve		Brayulinea densa	Blepharis maderaspatensis
Species		Commelina africanum	

Table 4.13. Continued. . .

		Commelina erecta	
		Crabbea hirsuta	
		Dicerocaryum zanguebarium	Justicia incerta
		Hermannia grisea	Lippea javanica
	Solanum panduraeforme	*Pentarrhinum* insipidum	Sida cordifolia
Temporary		Acanthosiceros naudiniana	
Species eaten	Blepharis maderaspatensis	Asparagus saunder*iae*	
only in the	*Felicia fasciularis*	Felicia fascicularis	
early part of	Hypoxis obtusa	Chaetacanthus costatus	
the Growing	Ruellia cordata	Phyllanthus parvulus	
Season	Solanum coccineum		Solanum coccineum
	Vernonia oligocephala		
Rejected or	Asparagus saunderiae	Achyrop*sis leptostachya*	Asparagus saunderiae
or *rarely*	Asparagus suaveolens		Borreria scabra
eaten		Blepharis maderaspatensis	Blepharis maderaspatensis
Species	Crabbea hirsuta	Cassia capensis	Commelina *africana*
		Commelina benghalensis	Commelina benghalensis
		Commelina ecklonianа	Commelina erecta
		Crotilaria pisicarpa	
	Evolvulus alsinoides	*Elephantorrhiza obliqua*	
	Fadogea monticola	Gomphrena celosioides	Gomphrena celosioides
	Hermannia boraginiflora	Hermbstaedtia odoreta	Hibiscus subreniformis
	Indigofera daleoides	Indigofera daleoides	
		Indigofera vicioides	Justicia spergulaefolia
		Justicia anagalloides	Justicia anagalloides
	Melhania prostrata	Oldenlandia herbacea	Oldenlandia herbacea
	Pavetta assimilis	*Pterococcus* africans	Pavonia transvaalensis
	P[illegible]ia capensis	Rhynchosia confusa	Phyllanthus parvulus
	P[illegible] insipidum	Rhynchosia venulosus	Portulaca quadrifida
	Salacia rehmannii	Ruellia cordata	*Solanum* panduraeforme
	Sida alba	Sida alba	
		Sida hoepfneri	Sida hoepfneri
		Tagetes minuta	Tagetes minuta
	Tephrosia forbesii	*Talinum caffrum*	
	Thunbergia neglecta	Thunbergia neglecta	
	Triumfetta sonderi	Triumfetta sonderi	

The third estimate of preference measured the duration of feeding on individual plants and hence the quantity of foliage eaten. The results obtained using this method generally significantly correlated with those obtained using the acceptance method, especially for the kudus. Thus the difference in time spent feeding on plants is not a serious problem for the measure of acceptance. A serious drawback of the feeding duration method was that it is affected by the size of the plant. The animals rarely fed on a plant for more than a few minutes before moving on to a different species. Hence the duration of feeding on large woody plants and clumped forbs may represent species selection, but for small bushes especially when the leaves are sparse, and for forbs growing in a dispersed pattern the feeding duration will be a reflection not only of the animals preference but of the size of individual plants.

All three techniques of measuring preference gave similar results, and often the measurements were significantly correlated. It was decided that the measurement of acceptance was the most suitable method of assessing species selection for the purpose of this study, which is to relate the selection of common plant species by browsing ungulates to the structural and chemical factors of these plants.

4. Species Selection

All the animals ate a wide range of plant species, rarely feeding for more than two minutes on any one plant before moving on to a different species. This highly diverse diet of large herbivores is well documented in the literature (Freeland & Janzen 1974, Westoby 1974, 1978), particularly for ungulates (Leuthold 1971, Conybeare 1975, Nge'the & Box 1976, Korfhage et. al. 1980, Grunow 1980, Novellie 1983), and for primates (Milton 1980, Glander 1981). The rapidity of switching from one plant species to another suggests that the feeding patterns are being determined by a need to avoid injesting deleterious quantities of plant secondary compounds (Arnold & Hill 1972, Freeland & Janzen 1974, Nagy & Reglin 1977, Westoby 1978, Marten 1978, Kuropat & Bryant 1979) rather than by nutrient constraints (Klein 1970, Westoby 1974, Pulliam 1975, Belovsky 1978) as it is unlikely that the animals require to balance their nutrient intake over such a short time scale, but the animals may have a very limited capacity to tolerate each type of toxin potentially present in the foliage.

Most of the preferred woody plants eaten in the growing season, such as _G._ _flavescens_ and _D._ _cinerea_ are deciduous. Thorny, microphyllous species like the _Acacias_ tended to be of low acceptance to the kudus when alternative foods are abundant, yet are favoured by the impalas which are of smaller body size.

In the dry season when the deciduous plants have shed their leaves the availability of foliage of these favoured species decreases and the herbivores must relax their preference criteria (Westoby 1974, Belovsky 1978) and eat more of the remaining species, since it is possibly more economical in terms of energy *conservation* to eat plants of a lower nutritional quality than to expend great amounts of energy in locating the few remaining plants of greater nutritional value. The standing crop biomass of both woody and herbaceous browse falls to 20% or less of the peak season biomass in savannas (Martins 1974, Novellie 1983). Since the majority of browse plants at Nylsvley are deciduous a similar decreased in biomass is to be expected. The acceptance of the deciduous plants which retain their old leaves on the stems, such as C. molle, increased in the early dry season, while that of the less favoured evergreen species increased as the dry season progressed and the favoured foods became more scarce. Evergreens are rarely favoured food species when other species are available (Leuthold 1970, Kuropat & Bryant 1980). The foliage of evergreens is often fibrous and frequently contains high levels of defensive compounds (Bryant et. al. 1983, Prudhomme 1983).

The forb species P. campestris was highly favoured by all the animals in the growing season, the impalas and goats also favoured T. forbesii. These and many other forbs die down in the dry season and so are not available to the animals. Several perennial forb species with fibrous stems showed an increased acceptance at this time.

Very few species of woody plants were totally rejected. Several of the forb species not eaten by the kudus and impalas are contain known toxins (Watt & Breyer-Brandwijk 1962). The goats did eat some of the poisonous forbs which were ignored by the indigenous animals.

One of the characteristic features of savannas is a pre-rain flush of woody plant foliage. This is attributed to the presence of sub-soil moisture which is available to the woody plants but not to the shallower rooted herbaceous plants, together with an increase in the photoperiod and temperature (Walker & Noy-Meir 1982). The immature leaves of some early flushing woody plants form an important source of food to the herbivores in September and October, even though the mature foliage may not be eaten, the prime example being D. pulchra. The impalas had a rather lower acceptance for these temporary food sources than the other animals. They preferred to feed on the new grass growth on the burned fire breaks. The early grass growth on burned areas is attributed to the increased temperature and light penetration when the shading effect of moribund grass is removed. The goats remained in a small home area which was not burned. Like the kudus, they had a high acceptance for new leaves of woody plants.

Plants such as D. rotundifolia which is only eaten in quantity when the leaves are either new or senescent are occasionally nibbled at other times, often for less than ten seconds. This suggests that the animals sample the plants in order to track the chemical changes taking place and possibly to prepare the rumen microflora for when the plant becomes edible (Glander 1981).

The goats restricted themselves to a small home area. This behaviour had several effects on their patterns of species selection. They responded more rapidly to the decline in availability of the preferred deciduous species, and more slowly to the increased abundance of palatable foods in the early growing season, than the indigenous animals. This is probably because their home area was heavily browsed and the supply of preferred foods was soon depleted once the growing season ended. The goats' habit of eating twigs bearing buds meant less edible vegetation was produced in the spring and they had to continue to use the evergreen species well into the growing season. A very noticeable difference between the feeding of the goats and the indigenous animals was the high preference and utilisation of the evergreen E. natalensis by the goats, particularly in the late dry season. At this time of year few other plant species remained in the goats area, consequentially they either had to eat this species or forage further afield.

4.5. SUMMARY OF RESULTS

a. Dietary Composition

i. Woody browse was the dominant vegetation component in the diet of the kudus at Nylsvley; very little grass was eaten.

ii. The impalas were preferential grazers of green grass. They ate a little browse throughout the year, increasing their use of woody plant leaves in the dry season when green grass was scarce.

iii. The goats were mixed feeders preferring browse. They ate considerably more grass than the kudus did in the growing season but, as for the kudus, woody plants formed the major component of the diet.

iv. Both the goats and the impalas increased their consumption of woody browse in the dry season, and much of that eaten was in the form of leaf litter. The kudus made only limited use of fallen leaves.

v. All the animals ate a greater proportion of woody browse than forbs.

vi. Fruit was actively sought out by all three animal species. Acacia seed pods were a favoured dry season food particularly for the impalas.

b. The Use of Browse Plant Species

i. The principal food species among woody plants during the growing season were _G. flavescens_, and for the kudus and impalas, _D. cinerea._

ii. Evergreen plants contributed little to the diet of the animals in the growing season but were eaten increasingly in the dry season. They made up a large proportion of the diet in the late dry season [illegible] deciduous browse was available.

iii. The goats ate more of the evergreen E. natalensis than the other animals in the dry season possibly due to depletion of the favoured species within their home range.

iv. Some woody plant species were not eaten throughout most of the year, yet formed an important temporary food source when in new leaf. These include B. africana, O. pulchra and D. rotundifolia.

v. Many forb species were eaten in small quantities. The use of several species of perennial forbs increased in the dry season. The goats alone ate some species of forbs known to be toxic.

c. Measuring Preference

i. The acceptance value is the most useful method of measuring species selection by browsing ungulates for comparison with quantitative measures of plant chemistry. Acceptance values are amenable to statistical analysis. Unlike the feeding duration acceptance is relatively unaffected by plant size.

d. Species Preference

i. Browse plant species could be categorised by the pattern of acceptance to browsing ungulates. In the growing season three main groups were observed:

i.) Favoured plants which were of consistantly high acceptance. These were generally deciduous species.

ii.) Intermediate species of moderate acceptance, generally comprising deciduous species and "thin-leaved" evergreens.

iii.) Non-preferred plants which were of very low acceptance if eaten at all. This group includes most of the "thick leaved" evergreen species.

Within the latter two categories are two further subgroups:-

a.) Dry Season Reserve species, used increasingly as the dry season progresses and the availability of the favoured deciduous plants decreases. The first species to increase in acceptance being the intermediate species, then in the late dry season some of the non-preferred species also increased in acceptance.

b.) Temporary species, usually eaten only when in new leaf but rejected once the leaves have matured.

e. Animal Species Differences

i. Differences in the patterns of acceptance by the goats, such as the earlier increase in the acceptance of many dry season reserve species and greater acceptance for E. natalensis, were probably attributable to their remaining in a small home range area in which depletion of the favoured plant species was evident, particularly in the dry season.

CHAPTER 5.

PLANT CHEMISTRY

5.1. INTRODUCTION

Plants contain a complex mixture of nutritive and anti-nutritive compounds within their tissues. Nutrients are defined as those compounds required by animals for normal growth, maintenance and reproduction. Protein, soluble carbohydrates and minerals are generally considered as nutrients, and occur mainly within the cell sap. The fibrous cell walls are partially available as energy sources to ruminants due to the production of cellulases by the rumen microflora (McBee 1971).

Plants also contain a variety of compounds originally termed plant secondary compounds, as they did not appear to be involved in the primary metabolic processes of the plants (Chew & Rodman 1979). Various functions were put forward for the presence of these compounds which often occur in high concentrations. Suggestions included waste products (Sachs 1887, Müller 1969, Luckner 1972), storage products (Blum & Ebercon 1976, Jager & Meyer 1977), growth and biosynthetic regulators, (Del Moral 1972, Fowden 1973, Nakanishi et.al. 1974, Robinson 1974), and radiation shields (McClure 1975, Rhoades 1977). The idea that these compounds might be involved in plant defence was first suggested by Stahl (1888) then again by Fraenkel (1959, 1969). There is still some debate on the adaptive significance of secondary compounds (Robinson 1974, Seigler & Price 1976, Seigler 1977), but generally it is accepted that a major function of secondary compounds is in defence against pathogens and herbivores (Rosenthal & Janzen 1979, Harborne 1978). That is not to say that these compounds are only of defensive significance to the plants, multiple functions are to be expected (Rhoades 1979). For example the phenolic resins of the creosote bush (Larrea tridentata) prevent damage by ultra violet radiation and dessication (Rhoades 1977). The same function is attributed to anthocyanins in immature Ochna pulchra leaves (Cresswell et.al. 1982). Many volatile terpenes are adapted to pollinators and fruit-dispersers (Dodson et.al. 1969, Brehm & Krell 1975).

Secondary chemicals have been proven to act against pathogens (Bell 1974, Deverall 1977), herbivores (Schoonhoven 1972, McKey 1974, Freeland & Janzen 1974, Beck & Reese 1976, Feeny 1976, Rhoades & Cates 1976) and against other plants (Rice 1974, 1977). However, some results are ambiguous due to the evolution of detoxification or tolerance mechanisms in specialised herbivores (Rhoades 1979, Levin 1979b).

The optimal defence theory (Rhoades 1979) states that organisms evolve and allocate defences in the way that maximises fitness. Defenses are costly, in terms of fitness, to the plant. Hence in the absence of herbivores the less well defended individuals will have the greatest fitness. The cost of defence is calculated, in terms of fitness lost, due to the resultant diversion of energy and nutrients from other needs into the synthesis, maintenance and storage of defence compounds. The commitment to defence is a positive function of the total nutrient budget of the plant. Plants should evolve defences in direct proportion to the risk of predation. Within the plant defences should be allocated in proportion to the risk of herbivory on that tissue and the value of that tissue, in terms of fitness lost, as a result of herbivory. Facultative production of defence compounds is to be expected as it is less costly than maintaining high levels of defence compounds in the absence of herbivory.

That the production of defence compounds lowers the growth and reproductive potential of plants has been shown many times in polymorphic populations. The acyanogenic morphs of Trifolium repens have a higher vegetative and sexual vigour than the cyanogenic morphs (Foulds & Grime 1972). Mutants of Nicotiana and Datura with especially high alkaloid contents are stunted (Mothes 1960). High yield crop plants are frequently very susceptible to pathogen and insect attack (Pimentel 1976). This suggests that energy and nutrients tied up in defensive chemicals are not available for growth. Inorganic nutrients are scarce and possibly often limiting to the growth of plants. Other than nitrogen, and silica in grasses, minerals are rarely present in defence compounds. Most defences are composed of carbon, oxygen and hydrogen.

It has been proposed by Feeny (1975, 1976) and Rhoades & Cates (1976) that the type of defence and degree of defensive commitment are directly related to the risk of discovery of plant tissues by herbivores. Feeny (1976) proposed the term quantitative defences for substances such as tannins and resins which act in a dosage dependent fashion. Quantitative defences are often present at high concentration (Feeny 1976, Rhoades & Cates 1976), up to 60% dry weight in the case of tannins.

Qualitative defences on the other hand are present in low concentrations, often less than 2% dry weight. They protect the plant against generalist herbivores, but offer little protection against specialised herbivores which have evolved detoxification or tolerance mechanisms.

Quantitative defences are characteristic of "apparent" plant tissues which are easy for the herbivore to locate, such as woody plants, particularly common, evergreen or late seral species and mature leaves. Qualitative defences are found in "unapparent" plants and tissues which tend to escape herbivory in time and space. These are the annual herbaceous species, rare, deciduous or early seral species and young leaves (Feeny 1976).

Rhoades and Cates (1976) point out that qualitative defences are mainly toxins directed against the metabolism of the herbivore e.g. alkaloids, while quantitative defences are designed to reduce the digestibility of the plant tissues. With qualitative defences a plant is at an advantage if it is chemically different from its neighbours but for quantitative defences, which are not easily overcome by herbivores, convergent evolution is common.

Defences are allocated to tissues according to their vulnerability and fitness value to the plant (McKey 1974). Young leaves and shoots are more valuable than mature leaves (McKey 1974) as the photosynthetic ability of leaves is highest when they have just reached full size (Freeland 1952, Roades & Wedding 1953, 1956, Syversten & Cunningham 1977, Mooney & Gulman 1982, Rowson & Wordward 1976, Krischick & Denno 1983). Loss of the terminal shoots may distort the growth form of the plant (McKey 1974). Defoliation at the time of flowering or seed production can severely reduce a plant's fitness. During the life time of a plant there may be drastic changes in the defensive requirements of different organs, and many defensive compounds are redistributed within the plant accordingly (McKey 1974).

If defences are costly it should be advantageous for plants to be less heavily defended in the absence of predators. The facultative production of increased levels of defence compounds in response to damage by herbivores has been recorded for alkaloids (Rhoades 1979), cyanogenic glycosides (Dement & Mooney 1974) phenolics (Theighs 1968, Haukioja & Niemèla 1976, 1977) and protease inhibitors (Green & Ryan 1972, Benz 1977). Induction times recorded vary from less than 12 hours to over a year. The short term response must be in qualitative defences as these are active in small quantities.

Stress, such as drought, increases the proximal nutrient content of plants (White 1969, 1974, 1976) due to disruption of normal metabolic patterns. This produces an imbalance in the nutrient quality of the plant and its defences. Qualitative defences tend to be increased and quantitative defences decreased (Rhoades 1983). Changes in the levels of glycosides (Bloem 1962), alkaloids (Jones 1950, Bloem 1962), essential oils (Mattson & Addy 1975) and tannins (Cooper-Driver et.al. 1977, Rhoades 1979) have been recorded.

The intuitive theory of costly and cheap defences has come under attack. Tannins and other "costly" quantitative defences have a slow turnover rate (Zucker 1983), but alkaloids and other qualitative defences show a rapid, and often daily, turnover rate (Robinson 1974). The half-life o[illegible]rpenes in Peppermint was only a few hours. Hence the cum[illegible]ost of quantitative and qualitative defences may be no different (Swain 1978), and for evergreen leaves tannins may even be cheaper (Fox 1981).

The difference between qualitative and quantitative defences is not absolute. A wide variety of terpenes are found in low concentrations in rain forest trees. (Lincoln and Langenheim 1976, Langenheim et.al. 1978), but in Eucalyptus species terpenes are quantitative defences forming 20% of the dry weight of the leaves (Morrow & Fox 1980). Similarly some toxins such as some cardiac glycosides and glucosinolates also have both toxic and digestion-reducing abilities (Chew & Rodman 1979).

It is possible 'hat small herbaceous plants contain toxins not because of cost differences, but because they need a rapid acting defence system (Fox 1981).

The cost of defence compounds depends on the nutritional state of the plants. Tannin and phenolics may cost a plant very little if they are growing in soils where nitrogen is limiting because the phenols may serve as a carbon sink for excess photosynthate (Phillips & Henshaw 1977).

Young leaves usually contain nitrogenous defences. This is generally though to be due to the problems of storing quantitative defences in actively dividing tissues (McKey 1974). However it may be because of a relative shortage of carbon in immature leaves until they reach their full photosynthetic potential. The young leaves of several plants growing in impoverished soils where nitrogen is limiting to growth contain carbon-based defences (Coley 1983, Rhoades & Cates 1976, Fox & Macauley 1977, McKey 1979, Crankshaw & Langenheim 1980, Langenheim et.al. 1980) presumably using carbon translocated from other parts of the plant. Plants growing in nitrogen poor habitats such as bogs (Romeo et.al. 1977) and subarctic habitats (Bryant et.al. 1983) rarely have nitrogenous defences. A positive correlation between mineral availability and concentrations of secondary chemicals containing them, has been established (Chew & Rodman 1979). The amount of sulphate given to Liliaceae and Cruciferaceae shows in the amount of sulphur containing isothyanates they produce, until a plateau is reached (Freeman & Mossadaghi 1970, 1971, 1972).

The allocation and type of defensive chemicals within a plant is a complex function of the risk of herbivory, the fitness value of the tissues and the nutrient budget of the plant. This is further complicated by the idea of plant defence guilds (Atsatt & O'Dowd 1976) whereby members of a plant community are affected by, and in many ways functionally dependent upon, the properties of other members of the plant community, i.e. a plant may gain protection from its association with other repellant plants as a non-discriminating herbivore will avoid the guild as a whole.

5.2. METHODS

The plant species chosen for chemical analysis were all abundant within the enclosure in which the tame animals were kept. The 14 woody plant species were chosen to give a range of utilisation by browsers (Witkowski 1980) and to represent a variety of plant families and growth forms. No previous study of the utilisation of the forb species by mammalian herbivores had been done so the 10 most common forb species were chosen.

Plant samples for analysis were collected from a fenced off area surrounding the weather station, immediately to the west of the enclosure. This area was protected from brow .ng but the plants were growing under a similar soil nutrient regime as those eaten by the tame animals. Composite samples collected from approximately 5 to 10 individuals of the same species were used in order to reduce variation due to individual differences. All collections were made between 7 and 9 a.m. before the ambient temperature became too high. Wilting is known to cause chemical changes in plants, particularly in cyanogenic glycoside levels and daily variation in alkaloid (Robinson 1974), moisture (Haukioja et.al. 1978) and nitrogen levels (Durzan 1968) are well documented.

The plants were then sorted into leaves and stems of a length which would be eated by the animals. Any foliage showing heavy insect damage or disease was discarded. In the field the animals rarely ate such leaves. The samples were washed briefly in deionised water to remove contaminating dust, then dried to constant weight in forced-draught ovens at 50-60'C.

Samples were collected for nutrient and fibre analysis from September 1980 to November 1981. The collection schedule for nutrient and fibre analysis was initially weekly in September and October when the new foliage was emerging and chemical changes were expected to be rapid, then every two weeks in November and December when young leaves were predominant, and in April and May at the start of the dry season. In the remaining months when chemical changes were probably less rapid, samples were collected on a monthly basis. The samples were analysed at the National Food Research Laboratories of the C.S.I.R. in Pretoria. Recurrent staffing problems lead to the number of analyses being halved and all the stem samples being grouped into two categories, as soft and hardened stems.

Samples were collected for secondary chemical analysis over the period September 1981 to August 1982. Samples of leaves of each phenological phase, i.e. new, young, mature, old and dried leaves, were collected. These samples were prepared in the same manner as the samples for nutrient and fibre analysis. Most of the tests were carried out by the researcher and a student assistant in the Department of Chemistry at the University of the Witwatersrand, Johannesburg. Analysis of condensed tannins were done by the researcher at the Sorghum Beer Unit, C.S.I.R. Pretoria and the analysis of total polyphenols was contracted out to the same unit.

1. *Nutrients*

Essential nutrients conventionally include water, energy, minerals, vitamins and amino-acids. For ruminants amino-acids are considered under the general nitrogen requirement because of the synthetic capabilities of the rumen microflora. The vitamin B complex and vitamin K are also synthesised by the rumen microflora. The vitamin C is destroyed in the rumen but the ruminant can synthesise this vitamin. Ruminants require external sources of the fat-soluble vitamins A, D and E, essential fatty acids and minerals (Van Soest 1982). The minerals regarded as essential in ruminant nutrition are nitrogen, phosphorus, potassium, calcium, magnesium, sodium and the trace elements. (Fleming 1973). Plant samples were analysed for the major cations.

a. Experimental

i. Nitrogen

The nitrogen content of the dried plant material was measured by the Kjeldahl procedure using a Kjeldahl-Foss Automatic Analyser. Proteins are converted to amino-acids, nitrate, then ammonium sulphate and hence to free ammonium which is dissolved in 4% boric acid and titrated with 0.1 N HCl to form NH_4Cl.

This procedure measures protein and nucleic-acids and is relatively unaffected by other nitrogen containing contaminants such as alkaloids. Crude protein is estimated as N x 6.25, as crude protein contains 16% nitrogen, but this is not absolutely accurate. The nitrogen content of plant proteins varies from 15% to 16% (Van Soest 1982). True protein is generally 10% less than the Kjeldahl crude protein estimate.

Yet the Kjeldahl technique is an improvement on Proximal analysis of nitrogen where the plant tissue is ashed before analysis. Proximal nitrogen includes inorganic N, free-amino acids, low molecular weight peptides, nucleic acids and alkaloids. The true protein content of the vegetation is 75 - 80% of the crude protein value calculated by proximal analysis (Van Soest 1982). The relationship between protein content and nutritional value is further complicated by fibre-bound proteins which may be indigestible to the animals. Between 1.5% and 2% of the nitrogen is bound to lignin in grasses and legumes, but the figure is much less for woody plants (Van Soest 1982).

ii. Phosphorus

The measurement of phosphorus is based on the destruction of all the organic matter and the conversion of organic phosphorus compounds to mineral phosphates by hydrolysis with hot 10N H_2SO_4 followed by hot 10N perchloric acid. The mineral phosphates are then converted to phospho-molybdates which on reduction with hydrazine sulphate give a blue colour which is measured colourimetrically against that of a known standard.

iii. Other Minerals

Samples for mineral analysis were ashed and hydrolysed with conc. HNO_3, then HCl. Lanthanum oxide in HCl was added to aqueous solution of the residual ash and the concentration of potassium, calcium, magnesium and sodium were measured by Atomic Absorption Spectroscopy using an air-acetylene flame. This technique uses the resonance lines in the atomic spectrum characteristic of each element. The Beer - Lambert Law states that the absorption is proportional to the concentration for a given absorption path length at any given wavelength.

2. Fibre

The main components of olant cell walls are the polysaccharides, cellulose and hemicellulose, and lignin which is a phenolic polymer.

Cellulose forms 4-50% of the dry mass of most plants. It is a polymer of glucose. Higher animals can only obtain energy from cellulose through intermediate microbial fermentation. The digestibility of cellulose varies from 0-100% depending on intrinsic factors such as the crystalinity of the cellulose and its association with lignin, cutin and silica. For this reason cellulose should not be considered nutritionally as a single substance. The fermentation rate of cellulose is affected by the plant species, the environment and maturity of the foliage (Van Soest 1982). Hemicellulose is more chemically diverse than cellulose being made up of xylose, arabinose, galactose or gluronic acid in a large array of linkages. The two main forms of hemicellulose are the pentosans, based on xylose, which form the bulk of the hemicellulose fraction of non-woody plants, and hexosans which are the main hemicellulose fraction of woody plants (Baily 1973).

The third component of the cell walls is lignin. Lignin is a high molecular weight phenolic polymer formed by the oxidation of cinnamyl alcohols. It cannot be degraded by either mammalian digestive enzymes or the rumen-flora. Lignin occurs in the mature cell walls of all vascular plants where it is distributed as a non-crystalline inclusion through out the entire cell wall. Lignin contributes to the stiffening and rigidity of the plant cell walls and internal structures (Swain 1979). Lignin also protects the plants against microbial attack by reducing the availability of digestible cell wall polysaccharides (Swain 1979). The lignin to cellulose ratio is the best indicator of digestibility of forage (Robbins & Moen 1975, Reed 1984).

Browsers have a shorter retention time than grazers as grass has a slow fermentation rate but contains relatively little lignin, while browsers cannot get any further nutrition from the lignin complexes in browse (Reed 1984).

a. Experimental

Fibre was estimated using Detergent Fibre Analysis. (Van Soest & Wine 1967). This technique is generally superior to proximate analysis in terms of partitioning cell-wall constituents into meaningful entities (Mould & Robbins 1981, Van Soest 1982). The method was developed for analysing cereals and graminoid feeds for livestock. Browse differs from many graminoids in that it contains significant amounts of cutin (Robbins et. al. 1975) and phenolic compounds (Feeny & Bostock 1968) which may bind to the fibre.

Total fibre as measured by neutral detergent fibre includes approximately 5% pectins which are fully digestible by ruminants and 20-30% of the protein, some of which are bound to the fibre, hence are probably digestible.

Approximately 23% of the hemicellulose is lost in the extraction. The use of sodium sulphide in the extraction procedure

reduces protein retention but may cause delignification and further loss of hemicellulose. In this study sodium lauryl sulphate was used to decrease contamination with residual protein.

Acid detergent fibre is a ligno-cellulose complex. This fraction also contains approximately 20% of the cell proteins. Phenolic substances form irreversible complexes with acid detergent fibre. Sequential extraction with neutral and acid detergents are less contaminated with protein (Mould & Robbins 1981) but unfortunately separate extractions were used for this study. Further extraction of the acid detergent fibre with H2SO4 removes the cellulose to give acid detergent lignins. Ashing this fraction gives a residue of cutin, silica and mineral ash and allows the estimation of lignin.

Hemicellulose in browse should be determined colourimetrically rather than by subtraction of acid detergent fibre from neutral detergent fibre (Mould & Robbins 1981).

3. Plant Secondary Compounds.

There are a vast range of highly diverse secondary compounds present in plants. The plant samples collected at Nylsvley were quantitatively analysed for enzyme-inhibiting polyphenols and condensed tannins, and screened for the presence of the major groups of toxic compounds, namely alkaloids, cyanogenic glycosides, mono- and sesqui-terpenes, saponins and ether - extractable compounds. Many other secondary compounds are also

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reduces protein retention but may cause delignification and further loss of hemicellulose. In this study sodium lauryl sulphate was used to decrease contamination with residual protein.

Acid detergent fibre is a ligno-cellulose complex. This fraction also contains approximately 20% of the cell proteins. Phenolic substances form irreversible complexes with acid detergent fibre. Sequential extraction with neutral and acid detergents are less contaminated with protein (Mould & Robbins 1981) but unfortunately separate extractions were used for this study. Further extraction of the acid detergent fibre with H2SO4 removes the cellulose to give acid detergent lignins. Ashing this fraction gives a residue of cutin, silica and mineral ash and allows the estimation of lignin.

Hemicellulose in browse should be determined colourimetrically rather than by subtraction of acid detergent fibre from neutral detergent fibre (Mould & Robbins 1981).

3. Plant Secondary Compounds.

There are a vast range of highly diverse secondary compounds present in plants. The plant samples collected at Nylsvley were quantitatively analysed for enzyme-inhibiting polyphenols and condensed tannins, and screened for the presence of the major groups of toxic compounds, namely alkaloids, cyanogenic glycosides, mono- and sesqui-terpenes, saponins and ether - extractable compounds. Many other secondary compounds are also

found in plants but these are either relatively rare such as cardiac glycosides, or like non-protein amino-acids and lectins, found most frequently in seeds. (Aplin 1976, Levin 1976a, Rosenthal & Janzen 1979).

i. Phenolic Compounds (*Tannins*)

Phenolic compounds are second only to carbohydrates in prevalence. They display great structural heterogeneity ranging from simple phenolics, based on a six carbon aromatic ring to complex polymeric structures such as tannins and lignins (Levin 1971). Most plants contain a complex mixture of phenolics. With the exception of the isoflavones which are estrogenic (Braden & McDonald 1970, Harborne 1979) and coumarins, which are hemorrhagic due to their anti-vitamin K activity (Levin 1976b, Van Soest 1982), simple phenolics are rarely toxic to herbivores (Levin 1971).

Polyphenols are however implicated in plant defence. Tannins are polyphenols with molecular weights between 500-3000, which have the special ability to precipitate proteins and polysaccharides (Bate-Smith & Swain 1962). Tannins fall into two chemically distinct classes, the hydrolyzable and condensed tannins. Much confusion has been caused in the literature pertaining to tannins because of the failure to realise the different modes of action of these two types of tannins.

Hydrolyzable tannins are divided into two types: The gallotannins which yield gallic acid upon hydrolysis, and the ellagitannins which yield ellagic acid. Both types of hydrolyzable tannins have a carbohydrate core. Specialist herbivores and microbes can degrade hydrolyzable tannins by hydrolyzing this carbohydrate core. Gallotannins are disk shaped molecules, while the spherical molecules of ellagitannins show greater structural diversity (Zucker 1983). This structural diversity of hydrolyzable tannins allows specificity towards proteins and other targets. This can be viewed as another sample of the co-evolutionary processes leading to the "arms race" between plants and their enemies. According to Zucker (1983) hydrolyzable tannins should be seen as specific inhibitors not generalised proteins digestibility reducing substances as envisaged by Rhoades & Cates (1976).

Condensed tannins contain no carbohydrate core and consequentially are less easily degraded. These helical molecules are derived from the condensation of flavonoid precursors called procyanadins and prodelphinidins. Condensed tannins are less structurally diverse than hydrolyzable tannins and probably act in a more generalised fashion (Zucker 1983).

Hydrolyzable tannins are stored in cell vacuoles but condensed tannins are bound to the cellulose, pectin and starches of the cell walls (Hagerman and Butler 1980).

Tannins complex with proteins (Van Sumere et. al. 1975), cellulose, pectin, starch and alkaloids (Swain 1965, Haslam 1979) by means of hydrogen, ionic and covalent bonds (Zucker 1983).

Condensed tannin complexes are more stable than those of hydrolyzable tannins and condensed tannins also bind more closely with cellulose (Swain 1956). The binding of condensed tannins decreases at pH values above 8 and that of hydrolyzable tannins at pHs above 5 (Van Sumere et. al. 1975).

It has been postulated that the major role of condensed tannins is to protect the plants from microbial and fungal attack (Swain 1978, Zucker 1983) since condensed tannins bind strongly with the proteins and polysaccharides found associated with the cell organelles (Swain 1965) and in the primary and secondary layers of the cell wall (McClure 1979, Swain 1979, Darvil et. al. 1980). These associations are relatively irreversible. Microbes exude exo-enzymes capable of utilising cellulose or pectin and hence breaching the cell walls. If condensed tannins are complexed with these substances the microbial enzymes will be deprived of binding sites (Zucker 1983). If the tannin complex persists after the leaves are shed they could serve to delay the breakdown of leaf-litter, thus preventing the loss of nutrients via too rapid seasonal leaching. (Zucker 1983). Condensed tannins may also inhibit the digestion of plants by ruminants through their effect upon microbial fermentation in the rumen (Waterman et. al. 1980). Insects obtain little food value from plant cell walls (Mattson 1980) so should be less affected by condensed tannins (Zucker 1983).

Hydrolyzable tannins are less inhibitory to microbes than are condensed tannins (Gustavson 1956, Pridham 1960, Feeny 1969).

Hydrolyzable tannins are more astringent than condensed tannins (Bate-Smith 1972). Astringency is caused by the binding of the glycoproteins in the mouth and is characteristic of tannins. Hydrolyzable tannins are not readily absorbed into the circulatory system. Their action upon herbivores is by the precipitation of digestive enzymes and the binding of food proteins (Zucker 1981). Ruminants can tolerate fairly high levels of hydrolyzable tannins due to the relatively alkaline conditions in the rumen and the hydrolysis of these substances by the rumenflora (McLeod 1970).

Tannins seem to be characteristic of perennial plants and are relatively rare in herbaceous species (Bate-Smith 1972). An estimated 80% of dicotyledonous woody perennials contain tannins as compared to 15% of the herbaceous species (Cates & Rhoades 1977). Condensed tannins are widely distributed in vascular plants, but hydrolyzable tannins are restricted to the dicotyledons (Swain 1976).

The seasonal distribution of the two types of tannins are reported to differ. Condensed tannins are probably synthesised according to microbial infection and degrade slowly (Zucker 1983). Hence they are at a maximum at the end of the growing season (Cooper-Driver et. al. 1977, Dement and Mooney 1974). Hydrolyzable tannins on the other hand are at a maximum in the early growing season when insect predation is heaviest and are degraded more rapidly (Feeny & Bostock 1968).

a. Experimental

i. Enzyme-inhibiting Polyphenols.

The enzyme inhibitory fraction of the total polyphenols in plants, which includes both hydrolyzable and condensed tannins, was measured by the Jerumanis method (Jerumanis 1972). Plant material was extracted in 75% dimethylformamide for one hour and centrifuged. This extracts polymeric phenols. The extract was then mixed with water, then 3.5% ferric ammonium citrate, then 8% ammonia solution. Polyphenols react with ferric ions in alkaline solution to produce a green/yellow dye. After 10 minutes the absorbance of the solution was determined at 525nm and compared to identically treated tannic acid standard . The results obtained by the Jerumanis method correlate well with the inhibition of grain enzymes due to the proteolytic activities of polyphenols (Daiber 1975).

This is in contrast to the more frequently used Folin-Denis reagent (A.O.A.C. 1980) for which no correlation between the total polyphenols measured and their ability to precipitate proteins was observed (Martin & Martin 1982, Van Soest 1982). The reactions were also affected by the degree of polymerisation of the phenolics (Swain & Goldstein 1965). The Folin-Denis reagent reacts with many phenols which do not precipitate proteins and several non-phenolic substances. In addition the more oxidised phenols are among the least reactive to this reagent. Another frequently used technique for determining total polyphenols is the relative astringency test (Bate-Smith 1973), where the ability to precipitate haemoglobin relative to a standard tannin is measured. This test needs a relatively high concentration of tannin before haemoglobin is precipitated and many plant extracts absorb light at the same wavelength as haemoglobin (Martin & Martin 1982).

ii. Condensed tannins

Condensed tannins were quantitatively measured by the Bate-Smith Proanthocyanidin method (Bate-Smith 1977) which involves the hydrolysis of condensed tannins into coloured flavonoid precursors which can be measured colourmetrically.

Conventionally this method involves extraction of plant material in hot aqueous methanol. However, this also extracts up to half the protein which binds with tannin. Using 70% acetone resolves this problem (Glennie pers. comm.). The acetone extract was concentrated to dryness and taken up again in a known volume of warm acetone. Condensed tannins were determined by heating an aliquot with n-butanol containing 5% HCl for two hours at 95 degrees C. This hydrolyses the condensed tannin into its coloured precursors procyanidin and prodelphinidin. The absorbance was then read over the range 545-560 nm. The standard used was Sorghum III tannin which is known to be condensed (Kaluza et.al. 1980). The American standard quebracho tannin was not available in South Africa.

Any other monomeric flavonoids present in the plant tissues may also be included in the colour reaction. Martin & Martin (1982) found that this method did not measure levels of extractable protein precipitating phenolics in graminoids, but condensed tannins in plants do have other functions (Zucker 1983). However, it does mean that subtracting condensed tannin from total polyphenols as measured by the Jerumanis method does not give a good estimation of the hydrolyzable tannin content.

Another frequently used technique of measuring for tannins is the vanillin - HCl method (Burns 1971). However this technique was found to be highly temperature dependent (Price et.al. 1978), and did not relate to the protein-precipitating abilities of poplyphenols (Daiber 1975).

Condensed tannins are rarely fully extractable from plant material. Damage to the cells prior to drying, and drying at temperatures much above 50 degrees C can combine tannins irreversibly with other cell wall polymers. Extraction also becomes more difficult as the foliage matures (Swain 1979).

ii. Alkaloids

Alkaloids occur in over 300 plant families and 7500 species (Li & Willaman 1972). They are found mainly in dicotyledonous species and only infrequently in gymnosperms and monocotyledons. Within the dicotyledons alkaloids are more prevalent in annual species than in perennial plants.

Alkaloids are a structurally diverse group of compounds incorporating nitrogen in a heterocyclic and / or aromatic ring. These compounds are usually synthesised from amino-acids (Robinson 1979). The primary site of synthesis is in the roots. The alkaloids are bound to sugars and transported to other sites within the plants, where they are stored in vacuoles (McKey 1974, Levin 1976). Some bound alkaloids may also be stored in the cytoplasm (Robinson 1979).

Within the plants alkaloids tend to be found in active tissues, epidermal layers, vascular sheaths and latex vessels (Robinson 1979). Alkaloid concentrations are affected by edaphic factors and such as climatic conditions and soil types (James 1950). In addition seasonal and diurnal changes occur (Robinson 1974, 1979). As with other "qualitative" defences alkaloid contents tend to be highest in young tissues, gradually declining with senescence (James 1950, Lee & Waller 1972, Robinson 1979).

There is a greater incidence of alkaloidal plants in the tropics and at low latitudes. This is attributed to the greater productivity and increased pest pressure in these sites (McNair 1935, Levin 1976).

The anti-microbial properties of alkaloids have been well documented in agricultural plants (Mitschner et.al. 1972, Roddick 1974, Levin 1976), as is the facultative production of alkaloids in response to tissue damage (James 1950, McKey 1974). Alkaloids are frequently highly toxic to many animals (Bull et. al. 1968, Schoonhoven 1972, Mattocks 1972, Culvenor 1973, Roddick 1974, Hedin et. al. 1974, Janzen et. al. 1977) although the effect on some insects is equivocal (Hanley & Thorsteinsen 1967, Levin 1976) as certain insects can detoxify specific alkaloids. Alkaloids have a bitter taste to mammals (Kingsbury 1964). Although not all alkaloids are toxic some can severely disrupt the animals metabolism through their action on the metabolism of:-

i.) DNA replication, RNA transcription and protein synthesis.

ii.) Membrane transfer processes.

iii.) Enzyme activity.

iv.) Blocking receptor sites for endogenous chemical transmitters.

v.) Affecting the conformation of other macro-molecules (Robinson 1979).

Alkaloids can be detoxified in small quantities by the mixed function oxidase system of animals and by the rumen-microflora (Kingsbury 1964). However, in some cases, such as the Senecio alkaloids, the metabolites are more toxic than the alkaloid itself (Mattocks 1972).

a. Experimental

Because alkaloids are so heterogeneous chemically, and there are so many of them, they cannot be identified in plant extracts using a single chromatographic criterion. However, a number of special "alkaloid reagents" have been devised for screening for alkaloids. Of these the most common are Dragendorff's reagent and Mayer's reagent (Robinson 1979).

Dragendorff's reagent is a solution of potassium tetraiodobismuthate which reacts to give a deep orange complex with many basic compounds including some non-alkaloids like choline (Bregoff et.al. 1953). It also reacts with a few non-basic substances especially carbonyl compounds (Farnsworth et.al. 1962). Dragendorff's reagent reacts with neutral alkaloids (Robinson & Fowell 1959) but not with common amino-acids (Winek & Fitzgerald 1961).

Mayer's reagent is potassium tetraiodomercurate (Cromwell 1955, Szasz & Buda 1971). It gives an off-white precipitate with alkaloids but also with some other types of plant constituents (Robinson 1979). This reagent works best in slighly acid solution.

The plant material was extracted with methanolic HCl (20ml methanol + 5ml 0.2m HCl) at room temperature for 24 hours. This was then evaporated to dryness and taken up in aqueous HCl.

i.) A drop of extract was applied to filter paper adjacent to a drop of Dragendorff's reagent (Raffauf 1962) and the darkening of the reagent noted in the area of fusion.

ii.) A few mls of solution were added to Mayer's reagent in a test tube and the formation of a precipitate noted.

Precipitation was quantified as cloudy (+) slight +, intermediate

++, strong +++.

iii. Cyanogenic Glycosides

Cyanogenesis is a widespread phenomenon in higher plants. The tissues of at least 100 plant families and 500 genera produce HCN when crushed (Gibbs 1974). Families noted for this phenomenon are the Rosaceae, Leguminosae, Gramineae, Araceae, Compositae, Euphorbiaceae and Passifloraceae. The cyanogenic potential of most plants may be attributed to one of 23 known cyanogenic glycosides (Seigler 1977).

Cyanogenic glycosides are prevalent in young tissues (Jones 1962, Rehr 1972). Genetic polymorphism is widespread in cyanogenic species (Jones 1971, Nass 1972, Cooper-Driver & Swain 1976, Harborne 1977, Conn 1979).

Cyanogenic glycosides are formed from a cyanogen (CN) molecule combined with a sugar. Upon hydrolysis prussic acid (HCN) is released (Alpin 1976). Cyanogenic glycosides are stored in vacuoles in the epidermal cells and the necessary hydrolysing enzymes are in the mesophyll cells (Conn 1979, Kojima et. al. 1979). Hence HCN is only liberated when the tissues are crushed. HCN combines irreversibly with the cytochrome oxidase enzymes leading to asphixiation at the cellular level (Lewis & Elvin-Lewis 1977, Conn 1979). Many insects are poisoned by HCN (Gilmour 1961, Keister & Beck 1964, Greshoff 1967) but some are able to detoxify it (Parsons & Rothschild 1964, Rehr et. al. 1973). Specialised insects such as the Heliconid butterflies even sequester cyanogenic glycosides from the food for their own defence (Gilbert 1971).

Cyanogenic glycosides are bitter to mammals and have often been the cause of stock losses (Kingsbury 1964). Ruminants are particularly susceptible to cyanide poisoning as the rumen microflora and the relatively high pH of the rumen promote hydrolysis (Moran 1954). Detoxification in mammals is by the enzyme rhodanase, which is situated mainly in the liver and kidneys. Some immunity to cyanide poisoning can be acquired but frequently the animals develop other symptoms such as goitre (Butler et. al. 1957).

a. Experimental

A small quantity of dried plant material was placed in a test tube with a drop of water, two drops of toluene and 1mg of emulsion (B-glucosidase). A picrate paper was suspended above the mixture and the tube firmly corked and left to incubate overnight at room temperature. Any release of HCN is detected by the darkening of the picrate paper (Harborne 1973). Certain volatile aldehydes and ketones as well as H_2S and SO_2 also discolour picric acid (Farnsworth 1966). A blank and a tube containing crushed almonds, rich in cyanogenic glycosides, were run as controls. The tests were repeated twice, once with a dry picrate paper and once with a wet paper.

iv. Saponins

Saponins have both toxic and digestion reducing properties (Ishaaya & Birk 1963). Saponins are the glycosides of triterpenes or sterols and have been found in over 80 plant families (Basu & Rastegi 1967). They are found in all parts of the plant but especially in the roots (Preston et. al. 1964). Saponin levels are low in immature tissues and are highest in mature leaves (Ishaaya & Birk 1965), and at the initiation of flowering. Saponin levels in plants decline as the plants senesce (Drozdz 1962, Marav'eva et. al. 1964).

Saponins alter the surface tension of the ruminal contents. This causes the gases produced by microbial fermentation to be trapped in froth causing rumen bloat (McCandlish 1937, Quin 1942, Olaron 1944, Lindahl et. al. 1954, 1957). The rumen microbes degrade saponins so ruminants are rarely poisoned by these substances. Saponins are not readily absorbed into the circulatory system but may enter through abrasion to the gut wall. Saponins have been proven to cause the death of sheep feeding on Alfombrella forage (Coburn-Williams 1978). Saponins containing medicagenic acid precipitate cholesterol (Gestetner et. al. 1971a & b). They have a strong haemolytic activity due to their ability to displace endogenous lipids from the lipoproteins of cell membranes (Gurd 1960), thereby causing the breakdown of cell membranes.

Saponins have some antimicrobial properties and interfere with water reabsorption in the hindgut of insects (Applebaum & Birk 1972, Applebaum et. al. 1969).

a. Experimental

The formation of persistant foams during extraction is reliable evidence that saponins are present (Harborne 1973). A simple test for saponins is to shake up an aqueous alcoholic plant extract in a test tube. The formation of a persistant foam indicates the presence of saponins. There is a good correlation between the amount of foam formed and the concentration of saponins present (O'Dell et. al. 1959). Saponins were also detected by thin layer chromatography (TLC) whereby plant extracts are separated out by selected solvents and identified by spraying with specific colour reagents.

Dried plant tissue was hydrolysed with 0.2M HCl for 4 hours. After cooling the solution was neutralised and the dried residue refluxed in hexane for 2 hours. The hexane was then evaporated off and the residue taken up in CHCl3. This solution was then subjected to TLC on silica gel in three separate solvents, CHCl3 - Me2CO (4:1) CHCl3 - EtoAc (1:1) and hexane - Me2CO3 (4:1). The best separation was achieved with hexane - Me2CO3 (4:1).

Saponins were then detected as pink and purple spots by spraying the plates with 5% antimony chloride in conc. HCl, and the heating at 110 degrees C for 10 minutes (Harborne 1973). Antimony chloride may also react with some terpenoids (Glennie pers. comm.).

v. Mono- and sesqui-terpenes

Like saponins terpenes have both toxic and digestion-reducing properties. Terpenoids represent one of the largest and biologically most important classes of natural products. They are found in all plants and show a great structural and functional diversity (Mabry & Gill 1979).

Terpenoids are based on the isoprene molecule and classified by the number of these C5 units they contain. Monoterpenes (C10) and sesquiterpenes (C15) are known as the essential oils. These are localised in the cytoplasm or in glandular cells. Among the plant families some of the richest in these compounds are the Compositae, Labiatae and Myrtaceae. Of the 900 known sesquiterpenes virtually all are restricted to the Compositae (Harborne 1973). These lower terpenes are usually bitter or pungent and occur in complex mixtures in the cells.

Mono- and sesqui- terpenes frequently have an antimicrobial function (Stroessel 1970, Rockwood 1974, Levin 1976b), for example the oils in citrus peel (Dabbah et. al. 1970). Monoterpenes have also been proven to inhibit the rumen microflora of deer, and hence inhibit digestion (Nagy et. al. 1964, Oh et. al. 1968, Radwan & Ellis 1975) while sesquiterpenes have been implicated in sheep losses (de Kock et. al. 1968, Witzel et. al. 1976). Essential oils are often harmful to insects (Burnett et. al. 1974, 1961). A well known natural insecticide is the monoterpene pyrethrin (Elliot & James 1973). Other functions of sesquiterpenes include allelopathic reactions by Artemisia species (McCohen et. al. 1973).

Many of the higher terpenes are also toxic. The diterpene glossypol in cotton and the irritant in the latex of Euphorbia species are examples (Mabry & Gill 1979). Toxic triterpenes include the lantadenes of some Lantana species (Hart et. al. 1976 a & b) and the exceedingly bitter curcurbitacins from members of the Cucurbitaceae (Mabry & Gill 1979).

a. Experimental

For the detection of mono- and sesqui- terpenes dried plant material was extracted in ether for an hour, then the filtrate was concentrated down and subjected to TLC in benzene : chloroform (1:1). The plates were irradiated by UV light, dark spots indicating the presence of terpenes. The plates were then sprayed with vanillin - H2SO4 reagent and heated at 100 degrees C for 10 minutes. Mauve to brown spots indicate the presence of mono- and sesqui- terpenes.

Replicate plates were sprayed with 2-4 dinitrophenyl hydrazine to detect terpenes with ketonic groups, which show as orange spots on a yellow background. Terpenes with double bonds were detected on the third set of replicate plates as red spots when the plates were exposed to bromine vapour after being sprayed with 0.05%

flourescein in water (Harborne 1973).

Control plates were run using prepared mono-terpenes: Carvone which has both a ketonic group and a double bond, citral and citronellal which have an aldehyde group and a double bond and terpineol with only a double bond (Marais pers. comm.).

vi. Ether-extractable Compounds

Ether extracts crude fats and terpenoid and phenolic resins and waxes from plant material (Bryant & Kuropat 1980, Van Soest 1982). Despite being an amorphous chemical grouping ether-extractable materials are frequently mentioned in feeding and digestion studies and have been important leads to finding the deterrent chemicals of browse in Northern America (Oh et. al. 1967, 1970, Radwan 1972) and Alaska (Bryant & Kuropat 1980).

a. Experimental

Dried plant material was extracted in ether overnight, then filtered and washed until the filtrate was colourless. The filtrate was then evaporated to dryness at room temperature and the residue weighed.

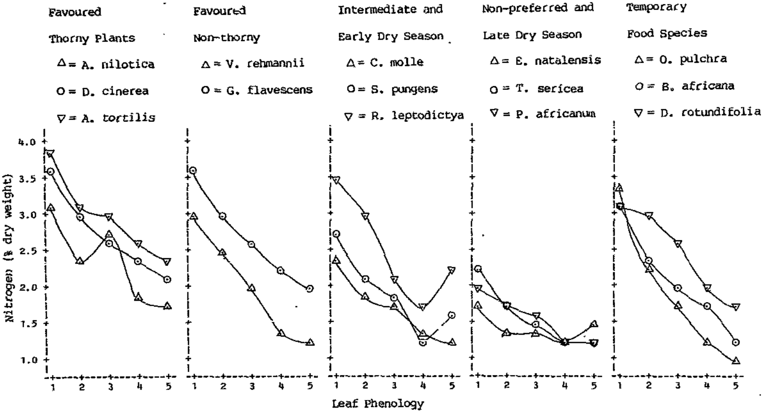
5.3. RESULTS

1. Nutrients

a. Woody plants

i. Nitrogen

The newly emerged leaves of woody plant species were rich in nitrogen. The highest were the new leaves of A. tortilis containing 3.9 ± 0.2% dry weight of nitrogen or 24.4% crude protein (Table 5.1.) The nitrogen concentration of the foliage decreased significantly as the leaves matured, then declined steadily throughout the year as the leaves aged (Fig 5.1). The initial decrease was particularly marked for O. pulchra. The new, red, leaves were rich in nitrogen but by maturity the nitrogen concentration of the leaves had halved. In the early dry season the leaves began to yellow. The nitrogen content of the richest species was 1.9 - 2.4% (12 - 16% protein) at this time and 1.2% (7.5% protein) for the poorest species. By the end of the dry season only a few dried leaves of the deciduous species remained on the bushes. Most of these leaves had an average nitrogen content of 1.3% (8% protein), although the dead leaves of the thorny species and D. rotundifolia still contained over 1.6% nitrogen (10% protein). The evergreen species E. natalensis and S. pungens had a nitrogen content of 1.5 and 1.6% respectively similar to that of the dried leaves of several deciduous species.



(1 = New leaves; 2 = Young leaves; 3 = Mature leaves; 4 = Old leaves; 5 = Dried leaves)

Fig 5.1. Changes in the concentration of Nitrogen *in the* leaves of *woody* plants throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.1. The Nitrogen Concentration (% Dry Weight) in Woody Plant Leaves and Stems

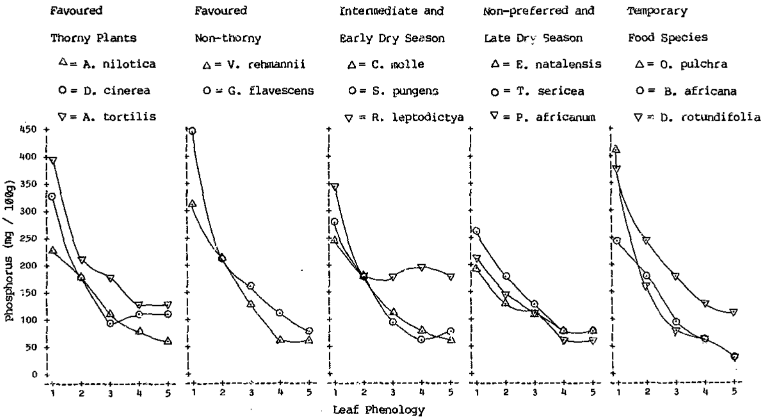
Species	New leaves Spring flush			Young leaves Oct to Dec			Mature leaves Jan to Mar			Old leaves Apr to June			Dried leaves July to Sept			Soft stems Oct to Dec			Hard stems Jan to Sept		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
Acacia nilotica	3.14±	0.20	4	2.39±	0.10	5	2.89±	0.35	3	1.93±	0.09	4	1.70±	–	1	2.01±	0.11	2	–	–	–
Acacia tortilis	3.90±	0.21	3	3.10±	0.12	7	2.97±	0.13	2	2.06±	0.07	4	2.40±	–	1	1.90±	–	1	–	–	–
Burkea africana	3.12±	0.09	3	3.53±	0.29	3	1.96±	0.04	4	1.78±	0.10	4	1.25±	0.40	2	1.62±	0.21	6	–	–	–
Combretum molle	2.44±	0.28	3	1.92±	0.07	6	1.65±	0.04	5	1.37±	0.03	3	1.30±	–	1	1.53±	0.15	10	0.80±	0.00	2
Dichrostachys cinerea	3.56±	0.10	3	2.97±	0.12	4	2.62±	0.12	2	2.35±	0.06	3	2.05±	–	1	1.63±	0.62	2	1.20±	–	7
Dombeya rotundifolia	3.15±	0.03	3	2.09±	0.20	4	2.58±	0.13	8	1.97±	0.09	3	1.70±	–	1	1.69±	0.11	9	0.95±	0.05	2
Euclea natalensis	1.79±	0.09	6	1.44±	0.11	10	1.44±	0.03	9	1.31±	0.06	6	1.47±	0.04	2	1.14±	0.09	15	0.95±	0.07	8
Grewia flavescens	3.89±	0.14	3	2.96±	0.04	3	2.59±	0.08	5	2.20±	0.11	4	2.00±	–	1	1.54±	0.10	6	0.59±	0.06	3
Ochna pulchra	3.41±	0.23	4	2.15±	0.12	7	1.76±	0.08	6	1.20±	0.11	4	1.08±	–	1	2.06±	0.26	6	1.08±	0.09	6
Peltophorum africanum	2.80±	0.12	3	1.81±	0.08	4	1.63±	0.15	3	1.53±	0.14	4	1.22±	–	1	1.42±	0.19	7	0.85±	0.05	2
Rhus leptodictya	3.49±	0.45	2	3.04±	0.17	5	2.14±	0.27	6	1.87±	0.25	6	2.30±	–	1	1.89±	0.10	6	1.23±	0.17	6
Strychnos pungens	2.	0.00	2	2.09±	0.14	3	1.92±	0.10	5	1.24±	0.09	5	1.64±	0.05	5	1.40±	0.14	5	0.87±	0.05	7
Terminalia sericea	2.16±	0.06	2	1.73±	0.04	5	1.54±	0.10	4	1.30±	0.12	3	1.30±	–	1	1.01±	0.06	3	0.70±	–	1
Vitex rehmannii	3.00±	0.09	3	2.46±	0.15	6	2.02±	0.10	5	1.40±	0.06	3	1.20±	–	1	1.27±	0.13	9	0.87±	0.04	2

The plants with the highest nitrogen contents in the mature leaves were the three thorny species A. nilotica, A. tortilis and D. cinerea, all of which are in the leguminous sub-family Mimosoideae. G. flavescens and D. rotundifolia were also rich in nitrogen. The leaves of all these species contained at least 2.5% nitrogen (16% protein). C. molle and the less favoured species, O. pulchra, P. africanum, T. sericea and the evergreen E. natalensis contained only 1.5% nitrogen (9 - 10% protein) in their mature leaves. The lowest protein content recorded for woody plant leaves was 6.2% for the dried leaves of O. pulchra.

The nitrogen content of stems was less than that of leaves. Soft new stems contained more nitrogen than the hardened stems. The soft shoots of D. rotundifolia, R. leptodictya and the thorny species contained around 2% nitrogen (10 - 13% protein) and those of V. rehmannii, E. natalensis and T. sericea contained only half this quantity. Hardened stems contained approximately 1.2 - 0.7% nitrogen. The hardened stems of D. cinerea and R. leptodictya were richest in nitrogen and those of C. molle and T. sericea poorest.

ii. Phosphorus

The seasonal pattern of distribution of phosphorus in woody plant foliage was similar to that of nitrogen, with the new leaves being rich in this mineral until they matured, and thereafter exhibiting a slow decline in phosphorus levels (Fig 5.2.).



(1 = New leaves; 2 = Young leaves; 3 = Mature leaves; 4 = Old leaves; 5 = Dried leaves)

Fig 5.2. Changes in the concentration of Phosphorus in the leaves of woody plants throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.2. The Phosphorus Concentration (mg / 100g) In Woody Plant Leaves and Stems

Species	New leaves Spring flush			Young leaves Oct to Dec			Mature leaves Jan to Mar			Old leaves Apr to June			Dried leaves July to Sept			Soft stems Oct to Dec			Hard stems Jan to Sept		
	Mean	*SE*	*n*	*Mean*	*SE*	*n*	*Mean*	*SE*	*n*	*Mean*	*SE*	*n*	*Mean*	*SE*	*n*	*Mean*	*SE*	*n*	*Mean*	*SE*	*n*
Acacia nilotica	343.8±	31.2	2	188.9±	22.6	4	123.4±	7.7	2	78.0±	5.0	7	62.0±	–	1	238.9±	–	1	–	–	–
Acacia tortilis	399.4±	28.3	3	217.3±	25.0	5	182.5±	7.1	3	182.5±	7.1	3	133.2±	2.5	4	137.0±	4.1	2	239.6±	–	1
Burkea africana	246.3±	9.3	3	188.0±	14.2	3	101.8±	10.8	3	58.6±	8.3	3	29.3±	3.8	3	156.3±	8.7	5	–	–	–
Combretum molle	254.0±	37.6	3	193.0±	19.1	6	107.1±	3.1	5	93.9±	6.0	4	61.0±	–	1	192.0±	21.7	6	113.3±	50.0	3
Dichrostachys cinerea	241.4±	36.4	3	213.4±	23.1	3	103.2±	8.6	2	107.2±	7.5	3	110.5±	–	1	152.5±	–	1	106.5±	–	1
Dombeya rotundifolia	392.1±	7.0	3	249.3±	45.9	4	186.0±	21.6	6	139.8±	2.2	5	106.0±	–	1	201.2±	14.0	7	108.4±	–	1
Euclea natalensis	219.7±	23.7	6	151.9±	14.8	12	108.2±	10.7	7	64.8±	6.8	6	77.1±	5.0	3	135.1±	9.1	12	85.9±	11.8	6
Grewia flavescens	313.1±	96.1	3	201.9±	4.3	4	161.7±	9.0	4	115.5±	16.8	4	83.0±	–	1	186.1±	4.6	4	121.3±	22.5	3
Ochna pulchra	412.0±	42.7	4	169.1±	27.1	7	98.9±	6.1	5	57.4±	7.8	4	28.0±	–	1	173.7±	16.1	4	114.3±	15.2	5
Peltophorum africanum	283.6±	12.5	3	144.4±	12.6	3	122.8±	27.0	5	88.2±	14.3	4	74.6±	–	1	205.9±	34.1	4	89.3±	22.8	3
Rhus leptodictya	345.0±	–	1	178.2±	43.8	5	193.1±	11.4	4	195.3±	43.8	5	177.2±	84.1	3	214.4±	31.4	3	138.8±	26.7	6
Strychnos pungens	286.4±	–	1	181.6±	19.9	3	101.8±	4.0	4	65.1±	5.8	5	78.9±	2.5	4	128.6±	16.4	5	55.6±	9.1	5
Terminalia sericea	255.0±	14.0	2	177.2±	9.0	6	128.3±	16.8	3	91.3±	1.1	4	90.7±	–	1	99.5+	–	1	58.0±	–	1
Vitex rehmannii	446.7±	137.1	3	214.9±	22.6	6	[illegible]	17.2	4	74.3±	8.7	3	58.0±	–	1	178.1±	23.4	6	118.1±	11.1	2

The new leaves of A. tortilis, D. rotundifolia and V. rehmannii were particularly rich in phosphorus, containing 450 - 390 mg/100g dry weight (Table 5.2.). As with nitrogen the phosphorus levels of O. pulchra foliage were very high in the new foliage but decreased rapidly as the leaves hardened. Immature leaves of E. natalensis and P. africanum contained only half the concentration of phosphorus found in the most mineral rich species.

A. tortilis, D. rotundifolia, G. flavescens and R. leptodictya contained the highest levels of phosphorus in their mature leaves. The concentration of phosphorus in R. leptodictya leaves did not show any decline after the leaves had reached full size, so by the late dry season this plant contained higher levels of phosphorus than were present in other species. In contrast the decline in phosphorus levels in B. africana and O. pulchra foliage was very marked. In the late dry season these plants contained less than 30 mg/100g of phosphorus. This is a 14 fold decrease in the phosphorus concentration of O. pulchra leaves. Most other plants showed a 2-4 fold decrease in phosphorus levels through out the year.

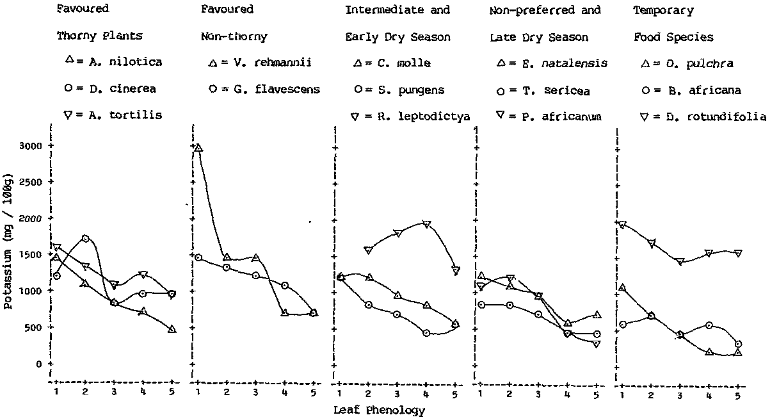
The soft new stems of woody plants contained less phosphorus than was found in the leaves, but more than in the hardened stems. New stems of the Acacia species were comparatively rich in phosphorus with 240mg/100g while those of T. sericea and the evergreen species contained half this amount. Once hardened the shoots of T. sericea contained only 58 mg/100g dry weight of phosphorus.

iii. Potassium

Potassium is found in relatively high concentrations in woody plants, again the highest concentrations tending to be found in immature leaves. After reaching full size the plants showed only a slow rate of decline in potassium concentrations, if any (Fig 5.3.).

The newly emergent leaves of D. rotundifolia and V. rehmannii were particularly rich in potassium (Table 5.3.). Other potassium rich species were A. nilotica, A. tortilis and G. flavescens with approximately 1500 mg/100g. The new leaves of T. sericea and B. africana contained only half this quantity. D. rotundifolia, V. rehmannii and G. flavescens continued to be rich in potassium once the leaves had matured, and contained at least 1200mg/100g of potassium. R. leptodictya was also rich in potassium. The two species containing the lowest potassium levels in their mature leaves were B. africana and O. pulchra with only 500 mg/100g. In the late dry season the semi-evergreen foliage of R. leptodictya was richer in potassium than most other plant species. There was no significant difference in the potassium concentration of the evergreen leaves and the dead leaves of several deciduous species in the late dry season.

Generally the woody plants contained more potassium in the leaves than in the stems, exceptions being the new stems of D.



(1 = New leaves; 2 = Young leaves; 3 = Mature leaves; 4 = Old leaves; 5 = Dried leaves)

Fig 5.3. Changes in the concentration of Potassium the leaves of woody plants throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.3. The Potassium Concentration (mg / 100g) in Woody Plant Leaves and Stems

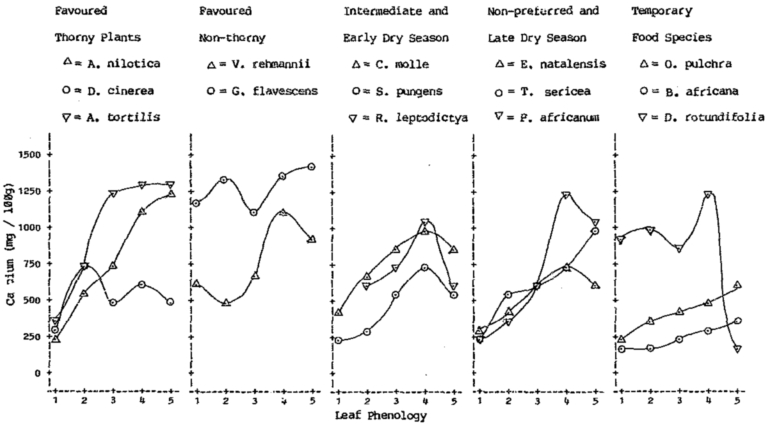
Species	New leaves Spring flush			Young leaves Oct to Dec			Mature leaves Jan to Mar			Old leaves Apr to June			Dried leaves July to Sept			Soft stems Oct to Dec			Hard stems Jan to Sept		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
Acacia nilotica	1516.9	±152.9	4	1110.7	± 82.1	4	887.2	± 83.3	2	750.1	± 95.4	4	472.0	± –	1	1338.6	± –	1	–	–	–
Acacia tortilis	1567.5	±176.3	3	1359.7	±311.1	5	1123.0	± 89.0	3	1209.6	±123.0	4	1063.8	±173.8	2	1203.4	± –	1	–	–	–
Burkea africana	678.1	±121.7	3	787.1	± 28.5	3	486.9	± 54.6	3	598.3	±105.6	3	424.1	±160.2	3	747.0	± 63.5	5	–	–	–
Combretum molle	1196.5	± 63.8	3	1311.8	± 63.9	6	1006.9	± 83.7	5	846.2	±129.1	4	622.0	± –	1	1331.1	±111.9	6	783.3	±288.4	3
Dichrostachys cinerea	1211.8	± 49.1	3	1707.2	±508.4	3	828.9	± 34.6	2	954.7	±205.4	3	1046.9	± –	1	1324.4	± –	1	882.0	± –	1
Dombeya rotundifolia	1958.5	±218.2	3	1739.8	±151.7	4	1515.8	±316.1	6	1652.7	± 32.5	5	1678.0	± –	1	2528.1	±197.8	7	1342.9	± –	1
Euclea natalensis	1260.1	± 30.7	6	1147.0	± 70.3	12	953.6	±124.9	7	632.7	± 40.4	6	769.7	±112.5	3	1502.8	±105.4	12	668.8	± 79.1	6
Grewia flavescens	1499.0	±222.2	3	1323.0	± 81.2	4	1215.9	± 18.0	4	1109.0	±116.5	4	768.0	± –	1	1479.8	±192.3	4	845.3	±260.4	3
Ochna pulchra	1167.3	± 87.2	4	685.9	±106.7	7	450.8	± 48.4	5	225.4	± 34.3	4	224.0	± –	1	1101.2	±105.8	4	617.9	±152.0	5
Peltophorum africanum	1114.1	± 98.9	3	1260.7	±246.1	4	957.5	±147.0	5	449.4	± 65.0	4	430.5	± –	1	1194.3	±193.9	4	849.7	±288.8	3
Rhus leptodictya	–	–	–	1629.5	±178.6	5	1861.0	±321.4	4	1955.5	±511.0	5	1407.0	±354.4	3	1890.0	±152.2	3	1317.9	±170.3	6
Strychnos pungens	1288.3	± –	1	909.1	± 84.1	3	700.6	±112.9	4	504.2	± 65.4	5	590.1	±109.6	4	1175.5	±154.9	5	440.8	± 74.9	5
Terminalia sericea	867.1	± 73.1	2	859.2	± 44.2	5	690.9	±148.8	3	508.8	± 34.5	4	539.1	± –	1	936.8	± –	1	477.0	± –	1
Vitex rehmannii	2936.9	±1421.3	3	1472.6	±104.3	5	1488.0	±152.2	4	808.7	± 49.1	3	701.0	± –	1	2304.1	±284.7	6	1090.2	±403.2	2

rotundifolia and E. natalensis and the hardened stems of O. pulchra. In these cases a slightly higher concentration of potassium was found in the stems than in the leaves.

iv. Calcium

The calcium concentration in the leaves of most woody plants showed the reverse seasonal change to the other cations, increasing as the leaves aged (Fig 5.4.). G. flavescens, and D. rotundifolia differed in that the calcium concentrations in the leaves were [illegible]y high and remained fairly constant throughout the year. [illegible] leaves of these species, and A. tortilis, C. molle and V. [illegible]ii were the richest in calcium with an excess of 400 mg/100g. The calcium concentration of mature A. tortilis leaves was very high at 1223 mg/100g. Other calcium rich mature leaves were of G. flavescens and D. cinerea. O. pulchra and B. africana were very low in calcium both as immature and mature leaves. P. africanum was also initially low in calcium but the accumulation of calcium by this plant was rapid increasing four fold over the year.

The stems, like the leaves, accumulated calcium as they hardened. Many species contained somewhat greater concentrations of calcium in the stems than the leaves. However the reverse pattern was shown by D. cinerea, G. flavescens and R. leptodictya. The stems of D. rotundifolia, C. molle and G. flavescens were the most rich in calcium.



(1 = New leaves; 2 = Young leaves; 3 = Mature leaves; 4 = Old leaves; 5 = Dried leaves)

Fig 5.4. Changes in the concentration of Calcium in the leaves of woody plants throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.4. The Calcium Concentration (mg / 100g) In Woody Plant Leaves and Stems

Species	New leaves Spring flush			Young leaves Oct to Dec			Mature leaves Jan to Mar			Old leaves Apr to June			Dried leaves July to Sept			Soft stems Oct to Dec			Hard stems Jan to Sept		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
Acacia nilotica	286.6	± 76.1	3	537.3	± 94.0	4	761.9	±174.3	2	1113.3	±124.4	4	1238.0	± –	1	320.9	± –	1	–	–	–
Acacia tortilis	402.4	± 38.6	3	780.0	±120.0	5	1223.3	±287.0	3	1323.5	±190.0	4	1336.1	± 48.1	2	424.6	± –	1	–	–	–
Burkea africana	[illegible]	± 41.7	3	175.9	± 24.8	3	283.9	± 86.8	3	337.8	± 44.1	3	368.1	± 29.5	3	458.7	± 93.4	5	–	–	–
Combretum molle	410.1	±119.8	3	667.9	±101.5	6	882.5	± 78.4	5	1023.2	±224.7	4	853.0	± –	1	1079.1	±246.5	6	899.0	±121.0	3
Dichrostachys cinerea	327.7	± 93.6	3	752.3	± 24.8	3	515.1	± 77.4	2	643.6	± 87.5	3	494.8	± –	1	158.4	± –	1	358.7	± –	1
Dombeya rotundifolia	935.9	±244.1	3	1011.9	±153.7	4	880.2	±114.2	6	1274.7	±133.5	5	1785.0	± –	1	1489.7	±112.7	7	1731.4	± –	1
Euclea natalensis	297.7	± 36.4	6	432.7	± 52.1	12	627.0	± 97.4	7	763.5	± 41.9	6	617.3	±101.3	3	495.8	± 43.6	12	911.3	±110.5	3
Grewia flavescens	1186.3	± 28.8	3	1034.4	± 96.6	4	1111.2	± 40.3	4	1386.7	±183.5	4	1453.0	± –	1	996.9	±[illegible]	4	899.4	±186.5	3
Ochna pulchra	243.7	± 79.3	4	347.6	± 56.4	7	427.1	± 32.3	5	498.6	± 3.6	4	605.0	± –	1	426.9	± 48.2	4	719.7	±113.7	5
Peltophorum africanum	284.4	± 26.6	3	365.9	± 21.0	4	639.4	±163.7	5	1243.8	±249.4	4	1077.4	± –	1	428.4	± 50.1	4	595.3	±139.7	3
Rhus leptodictya	–	–	–	600.2	±106.7	5	757.1	± 42.6	4	1063.9	±158.8	5	611.7	±150.3	3	360.4	± 25.1	3	516.8	± 58.3	6
Strychnos pungens	278.9	± –	1	324.7	± 72.6	3	588.0	±119.8	4	766.9	±105.3	5	560.3	± 60.3	4	352.0	± 46.6	5	516.3	± 99.0	5
Terminalia sericea	278.1	± 62.9	2	585.3	± 86.3	5	596.1	±161.0	3	724.6	± 66.6	4	989.3	± –	1	597.9	± –	1	164.4	± –	1
Vitex rehmannii	643.3	±342.8	3	489.9	± 85.8	6	670.6	±113.4	4	1103.0	± 90.7	3	940.0	± –	1	516.6	± 65.7	6	605.6	±119.4	2

v. Magnesium

The magnesium concentration in the leaves remained fairly constant throughout the year (Fig 5.5.). The richest plants were G. flavescens, V. rehmannii, D. rotundifolia and C. molle with 350-400 mg/100g, while O. pulchra and B. africana contained only 160-100 mg/100g (Table 5.5.). In the dry season D. cinerea, R. leptodictya and P. africanum were also among the magnesium-rich species.

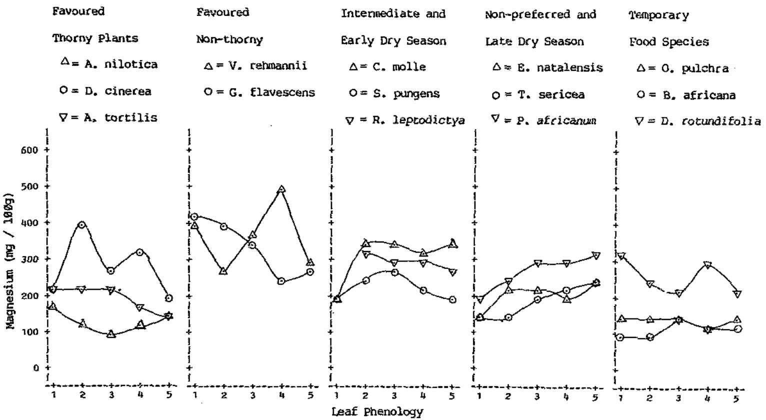
The species containing most magnesium in their leaves also had the highest levels of magnesium in their stems. For most species the concentration of magnesium in the leaves was greater than that in the stems, but the opposite pattern was evident for B. africana, D. rotundifolia and E. natalensis.

vi. Sodium

Very little sodium was detected in woody plants. The concentration in the leaves was always below 10 mg/100g (Table 5.5.). Little difference was detected between plant species or plant parts, but generally A. tortilis and D. rotundifolia appeared to be slightly richer in sodium than B. africana and T. sericea (Fig 5.6.).

vii. Moisture

The moisture content of the foliage of all woody species decreased



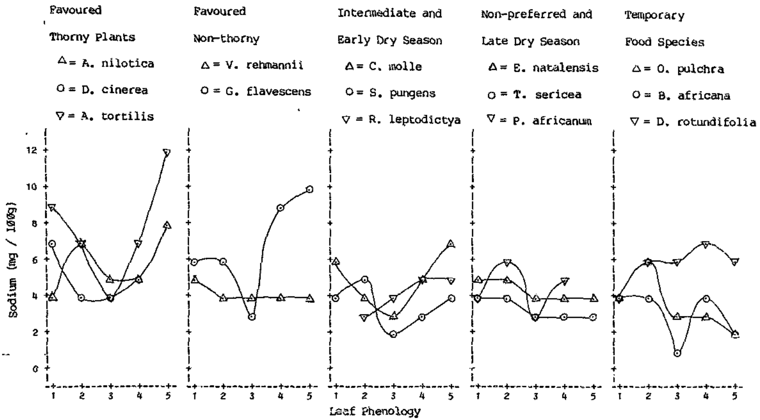
(1 = New leaves; 2 = Young leaves; 3 = Mature leaves; 4 = Old leaves; 5 = Dried leaves)

Fig 5.5. Changes in the concentration of Magnesium in the leaves of woody plants throughout the year.

Plants grouped according to their acceptance to browsing ungulates.

Table 5.5. The Magnesium Concentration (mg / 100g) in Woody Plant Leaves and Stems

Species	New leaves Spring flush			Young leaves Oct to Dec			Mature leaves Jan to Mar			Old leaves Apr to June			Dried leaves July to Sept			Soft stems Oct to Dec			Hard stems Jan to Sept		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
Acacia nilotica	172.7 ±	30.0	3	124.4 ±	16.4	5	99.2 ±	4.2	2	116.8 ±	11.3	4	148.0 ±	–	1	177.6 ±	–	1	–	–	–
Acacia tortilis	216.1 ±	25.3	3	231.0 ±	11.9	5	216.7 ±	9.2	3	174.4 ±	13.4	4	142.3 ±	3.8	2	133.1 ±	–	1	–	–	–
Burkea africana	104.9 ±	13.1	3	107.1 ±	5.1	3	141.3 ±	24.7	3	119.9 ±	21.4	3	125.1 ±	10.0	3	150.1 ±	9.1	5	–	–	–
Combretum molle	194.5 ±	37.4	3	335.2 ±	25.9	6	349.1 ±	33.3	5	332.7 ±	28.4	4	341.0 ±	–	1	335.5 ±	12.0	6	318.7 ±	16.4	3
Dichrostachys cinerea	223.4 ±	13.5	3	397.2 ±	97.5	3	284.7 ±	74.4	2	319.9 ±	55.7	3	186.1 ±	–	1	145.5 ±	–	1	129.1 ±	–	1
Dombeya rotundifolia	324.7 ±	54.5	3	257.3 ±	11.2	4	348.8 ±	35.9	6	292.1 ±	60.7	5	220.0 ±	–	1	411.4 ±	33.6	7	492.2 ±	–	1
Euclea natalensis	135.0 ±	17.0	6	159.7 ±	14.5	12	191.0 ±	18.1	7	233.2 ±	32.5	6	246.8 ±	24.0	3	233.8 ±	59.1	12	291.5 ±	66.1	6
Grewia flavescens	406.2 ±	24.3	3	403.2 ±	10.0	4	354.6 ±	22.4	4	258.1 ±	5.1	4	272.0 ±	–	1	382.2 ±	11.0	4	388.0 ±	17.0	3
Ochna pulchra	159.2 ±	17.7	4	148.5 ±	7.7	7	145.4 ±	4.2	5	123.2 ±	12.0	4	143.0 ±	–	1	189.2 ±	19.0	4	169.5 ±	29.7	5
Peltophorum africanum	204.9 ±	18.5	3	236.2 ±	36.4	4	292.6 ±	33.1	5	306.9 ±	60.0	4	316.0 ±	–	1	259.8 ±	50.6	4	258.0 ±	32.3	3
Rhus leptodictya	–	–	–	324.2 ±	115.7	5	308.5 ±	46.9	4	295.6 ±	14.8	5	266.5 ±	38.1	3	169.5 ±	47.1	3	18[illegible].4 ±	42.5	6
Strychnos pungens	212.0 ±	–	1	235.7 ±	14.8	3	279.3 ±	30.1	4	216.3 ±	25.7	5	281.5 ±	35.0	4	290.5 ±	34.5	5	163.3 ±	21.4	5
Terminalia sericea	154.6 ±	6.0	2	230.6 ±	16.4	5	215.9 ±	16.9	3	204.8 ±	7.4	4	239.7 ±	–	1	108.2 ±	–	3	143.0 ±	–	1
Vitex rehmannii	427.1 ±	154.4	3	274.9 ±	24.6	6	383.3 ±	42.5	4	514.7 ±	46.1	3	287.0 ±	–	1	295.3 ±	22.2	6	235.5 ±	20.5	2

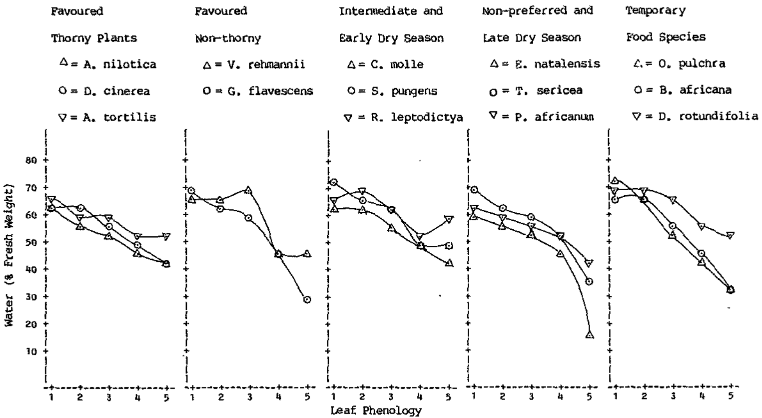


(1 = New leaves; 2 = Young leaves; 3 = Mature leaves; 4 = Old leaves; 5 = Dried leaves)

Fig 5.6. Changes in the concentration of Sodium in the leaves of woody plants throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.6. The Sodium Concentration (mg / 100g) in Woody Plant Leaves and Stems

Species	New leaves Spring flush Mean ± SE	n	Young leaves Oct to Dec Mean ± SE	n	Mature leaves Jan to Mar Mean ± SE	n	Old leaves Apr to June Mean ± SE	n	Dried leaves July to Sept Mean ± SE	n	Soft stems Oct to Dec Mean ± SE	n	Hard stems Jan to Sept Mean ± SE	n
Acacia nilotica	4.3 ± 0.9	3	6.6 ± 1.0	4	4.5 ± 0.6	2	5.2 ± 1.0	5	7.5 ± -	1	9.5 ± -	1	- -	-
Acacia tortilis	8.7 ± 1.0	3	6.5 ± 1.5	5	3.6 ± 0.6	2	6.8 ± 1.5	4	10.6 ± 0.5	2	6.1 ± -	1	- -	-
Burkea africana	3.7 [illegible]	3	3.7 ± 1.0	3	1.3 ± 0.9	3	3.8 ± 1.5	3	1.0 ± 0.5	2	5.8 ± 1.6	5	- -	-
Combretum molle	5.7 ± [illegible]	3	4.4 ± 0.6	5	3.3 ± 0.4	5	5.2 ± 1.6	4	7.3 ± -	1	4.6 ± 0.6	5	5.0 ± 1.1	3
Dichrostachys cinerea	6.8 ± 1.3	3	3.5 ± 0.6	3	3.8 ± 0.4	2	4.9 ± 1.2	3	- -	-	0.6 ± -	1	3.3 ± -	1
Dombeya rotundifolia	3.7 ± 0.7	3	6.3 ± 1.4	4	5.6 ± 1.7	6	6.7 ± 0.9	6	5.9 ± -	1	6.0 ± 1.1	6	3.9 ± -	1
Euclea natalensis	4.6 ± 0.5	5	5.1 ± 0.6	10	3.5 ± 0.8	7	3.6 ± 0.7	6	4.4 ± 0.0	2	4.4 ± 0.6	12	4.2 ± 0.6	6
Grewia flavescens	6.2 ± 0.7	3	6.1 ± 1.3	3	3.0 ± 0.5	4	8.3 ± 2.3	4	10.2 ± -	1	4.5 ± 1.6	3	4.1 ± 0.7	3
Ochna pulchra	4.4 ± 0.2	3	5.6 ± 1.4	6	3.2 ± 0.8	5	2.9 ± 1.4	2	2.4 ± -	1	[illegible].2 ± 0.6	3	6.2 ± 1.4	5
Peltophorum africanum	3.6 ± 1.0	3	6.0 ± 2.4	4	2.8 ± 0.6	5	4.7 ± 1.6	3	- -	-	5.2 ± 0.5	4	4.1 ± 0.7	3
Rhus leptodictya	- -	-	3.3 ± 0.3	4	4.3 ± 0.6	4	4.6 ± 0.9	5	5.0 ± 1.3	3	3.9 ± 0.6	3	4.7 ± 0.8	6
Strychnos pungens	3.8 ± -	1	5.3 ± 1.1	3	2.3 ± 0.6	4	3.1 ± 0.3	5	3.9 ± 1.0	2	4.7 ± 0.9	5	5.2 ± 1.3	3
Terminalia sericea	3.6 ± 0.5	2	3.5 ± 0.9	5	2.9 ± 0.3	2	3.2 ± 0.8	4	3.1 ± -	1	5.0 ± -	1	3.8 ± -	1
Vitex rehmannii	5.0 ± -	1	4.0 ± 0.7	5	4.4 ± 1.1	4	4.4 ± 1.4	3	3.7 ± -	1	5.4 ± 1.0	5	4.4 ± 0.1	2



(1 = New leaves; 2 = Young leaves; 3 = Mature leaves; 4 = Old leaves; 5 = Dried leaves)

Fig 5.7. Changes in the concentration of Water in the leaves of woody plants throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.7. The Moisture Content (% Fresh Weight) of Woody Plant Leaves and Stems

Species	New leaves		Young leaves		Mature leaves		Old leaves		Dried leaves		Fallen leaves		Soft stems		Hard stems	
	Spring flush		Oct to Dec		Jan to Mar		Apr to June		July to Sept		July to Sept		Oct to Dec		Jan to Sept	
	Mean SE	*n*	*Mean SE*	*n*	*Mean SE*	*n*	*Mean SE*	*n*	*Mean SE*	*n*	*Mean SE*	*n*	*Mean SE*	*n*	*Mean SE*	*n*
Acacia nilotica	63.5 ± 2.0	6	55.8 ± 1.2	5	54.8 ± 2.9	5	47.7 ± 1.0	7	44.0 ± -	1	33.0 ± -	1	60.0 ± 6.7	3	44.5 ± 2.5	2
Acacia tortilis	65.5 ± 1.0	4	60.4 ± 1.3	7	61.4 ± 1.6	5	53.0 ± 0.8	10	52.0 ± -	1	41.0 ± -	1	62.0 ± 3.0	2	45.0 ± -	1
Burkea africana	65.2 ± 0.9	5	65.7 ± 0.3	3	58.3 ± 2.1	6	46.6 ± 3.1	5	32.7 ± 4.7	6	28.0 ±16.0	2	63.4 ± 2.1	10	- -	-
Combretum molle	63.4 ± 2.5	5	62.9 ± 1.2	8	55.1 ± 1.0	7	49.6 ± 3.1	5	44.0 ± 2.0	2	13.0 ± 1.0	2	60.7 ± 2.6	13	43.5 ± 1.5	10
Dichrostachys cinerea	63.7 ± 3.3	3	62.2 ± 0.9	5	56.5 ± 1.7	4	51.2 ± 1.5	6	42.8 ± 4.1	4	14.0 ± -	1	61.0 ± 4.6	4	42.0 ± 5.5	3
Dombeya rotundifolia	69.5 ± 1.5	6	68.8 ± 1.5	4	65.2 ± 1.5	9	55.4 ± 1.5	7	52.0 ± 0.0	2	11.0 ± 1.0	2	63.8 ± 1.7	14	53.4 ± 1.7	8
Euclea natalensis	59.5 ± 0.8	14	57.7 ± 1.3	10	53.2 ± 1.7	10	48.1 ± 1.0	10	15.5 ± 6.5	4	35.0 ± -	1	59.6 ± 1.5	28	43.6 ± 3.7	17
Grewia flavescens	71.0 ± 2.0	2	64.2 ± 1.0	5	61.1 ± 0.8	7	47.0 ± 1.5	7	31.0 ±11.2	3	21.0 ± -	1	57.8 ± 3.0	6	48.5 ± 2.3	12
Ochna pulchra	73.6 ± 1.2	5	65.9 ± 2.4	7	54.7 ± 2.0	10	41.9 ± 1.7	8	34.0 ± 1.0	2	48.0 ± 3.0	2	63.2 ± 4.5	9	49.3 ± 1.7	16
Peltophorum africanum	62.6 ± 1.4	5	60.1 ± 0.5	4	55.5 ± 1.3	6	53.4 ± 0.8	8	43.0 ± -	1	14.0 ± -	1	61.3 ± 1.3	11	47.8 ± 0.7	8
Rhus leptodictya	65.3 ± 2.1	4	69.5 ± 1.6	4	63.6 ± 1.6	10	52.7 ± 3.7	9	59.0 ± -	1	11.0 ± -	1	69.4 ± 3.4	9	52.2 ± 0.5	15
Strychnos pungens	74.0 ± -	1	66.5 ± 3.5	2	61.9 ± 2.0	8	50.9 ± 1.0	9	49.0 ± 1.5	5	39.0 ± -	1	58.7 ± 1.7	3	49.8 ± 1.5	17
Terminalia sericea	71.0 ± 5.0	3	62.3 ± 1.1	6	60.6 ± 0.4	5	52.6 ± 1.4	8	36.5 ± 7.5	2	13.0 ± -	1	62.0 ± 3.2	4	48.7 ± 2.9	9
Vitex rehmannii	68.0 ± 5.5	3	66.5 ± 2.4	8	68.4 ± 1.4	7	48.0 ± 3.8	5	47.6 ± 2.7	3	22.0 ± -	1	68.8 ± 2.2	12	49.3 ± 2.4	1

steadily as the leaves aged (Fig 5 7.). The species with the highest moisture content in the leaves were V. rehmannii, D. rotundifolia and R. leptodictya in the wet season with 64-68% moisture, while A. nilotica and E. natalensis contained only 53-58% moisture (Table 5.7.). In the late dry season the same species continued to contain the most water but the dead leaves of E. natalensis, G. flavescens and B. africana contained less than a third of their weight in water.

viii. Relationship between Nutrients

In woody plant foliage there was a strong positive correlation between phosphorus and nitrogen and between phosphorus and potassium (Table 5.8.). Correlations of these nutrients with calcium and sodium were weaker but still positive. Magnesium was relatively independent of other nutrients and was only correlated to potassium and calcium in the immature foliage. The moisture content of the foliage showed a weak positive correlation with potassium and magnesium in the late wet season and with potassium and phosphorus in the dry season.

ix. Distribution of Nutrients between Plant Species

A. tortilis, D. rotundifolia and G. flavescens were comparatively rich in all nutrients. The three thorny or spiny species and new O. pulchra leaves were notably rich in nitrogen. R. leptodictya foliage contained much phosphorus, potassium and magnesium while leaves of C. molle and V. rehmannii were rich in calcium.

Table 5.8. Intercorrelations Between the Nutrient Concentrations in Woody *Plant Leaves*

i. New Leaves

	Nitrogen		Phosphorus		Potassium		Calcium		Magnesium		Sodium	
	r	n	r	n	r	n	r	n	r	n	r	n
Phosphorus	0.613*	13										
Potassium	0.249	13	0.722**	13								
Calcium	0.347	13	0.377	13	0.532	13						
Magnesium	0.350	13	0.521	13	0.807***	13	0.859***	13				
Sodium	0.591*	13	0.233	13	0.180	13	0.209	13	0.239	13		
Water	0.332	14	0.482	13	0.110	13	0.287	13	0.300	13	-0.105	13

ii. Young Leaves (October to December)

	Nitrogen		Phosphorus		Potassium		Calcium		Magnesium		Sodium	
	r	n	r	n	r	n	r	n	r	n	r	n
Phosphorus	0.725**	14										
Potassium	0.604*	14	0.577*	14								
Calcium	0.599*	14	0.677**	14	0.683**	14						
Magnesium	0.456	14	0.362	14	0.680**	14	0.674**	14				
Sodium	0.081	14	0.102	14	-0.034	14	0.275	14	-0.232	14		
Water	0.390	14	0.328	14	0.197	14	0.057	14	0.329	14	-0.373	14

iii. Mature Leaves (January to March)

	Nitrogen		Phosphorus		Potassium		Calcium		Magnesium		Sodium	
	r	n	r	n	r	n	r	n	r	n	r	n
Phosphorus	0.607*	14										
Potassium	0.332	14	0.304	14								
Calcium	0.571*	14	0.754**	14	0.561*	14						
Magnesium	0.067	14	0.292	14	0.660*	14	0.403	14				
Sodium	0.420	14	0.415	14	0.694**	14	0.421	14	0.314	14		
Water	0.328	14	0.423	14	0.633*	14	0.265	14	0.591*	14	0.343	14

Table 5.8. Continued. . .

iv. Old Leaves (April to June)

	Nitrogen		Phosphorus		Potassium		Calcium		Magnesium		Sodium	
	r	n	r	n	r	n	r	n	r	n	r	n
Phosphorus	0.534*	14										
Potassium	0.584*	14	0.928***	14								
Calcium	0.516	14	0.537*	14	0.664**	14						
Magnesium	-0.088	14	0.224	14	0.282	14	0.226	14				
Sodium	0.766*	14	0.530	14	0.594*	14	0.719**	14	0.158	14		
Water	0.232	14	0.623*	14	0.541*	14	0.247	14	0.298	14	0.267	14

v. Dried Leaves (July to September)

	Nitrogen		Phosphorus		Potassium		Calcium		Magnesium		Sodium	
	r	n	r	n	r	n	r	n	r	n	r	n
Phosphorus	0.830***	14										
Potassium	0.678**	14	0.791**	14								
Calcium	0.215	14	0.210	14	0.394	14						
Magnesium	-0.181	14	0.139	14	0.103	14	0.154	14				
Sodium	0.669**	11	0.484	11	0.303	11	0.630*	11	0.020	11		
Water	0.430	14	0.573*	14	0.511	14	0.264	14	0.042	14	0.496	11

(Significance Levels : * P < 0.05; ** P < 0.01; *** P < 0.001)

The matured leaves of B. africana and O. pulchra were of low nutrient content, often containing less than half the mineral content of the most nutrient rich species. C. molle, T. sericea and P. africanum were low in nitrogen, in addition P. africanum and E. natalensis contained relatively little phosphorus.

The nutrient status of stems usually reflected that of the leaves. Stems of E. natalensis and T. sericea were particularly poor in nutrients and R. leptodictya stems were comparatively mineral rich.

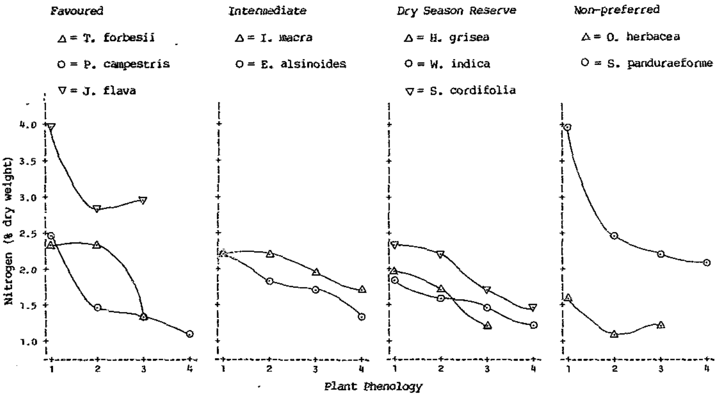
b. Forbs

i. Nitrogen

The nitrogen content of whole forbs was highest in immature plants and declined as the plants aged (Fig 5.8.). J. flava and the spiny forb S. panduraeforme were particularly rich in nitrogen (Table 5.9.). The preflowering plants contained 4% nitrogen (25% protein), decreasing to 3% and 2.1% respectively by the end of the year. The forb with the lowest nitrogen content was O. herbacea having only 1.6 - 1.1% nitrogen (7-10% protein).

ii. Phosphorus

Most forbs displayed a gradual de... their phosphorus content as the plants aged (Fig 5.9.). Pla... richest in

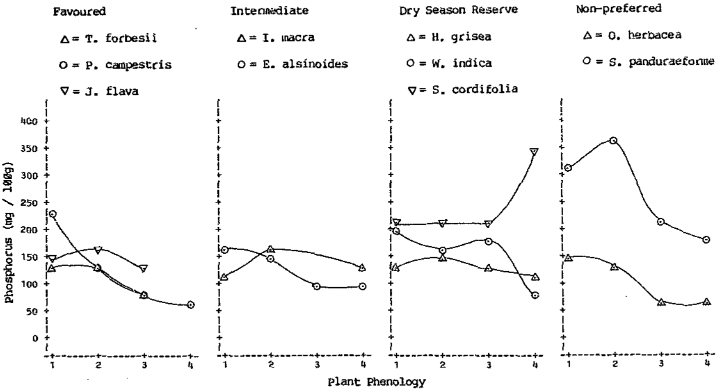


(1 = Pre-flowering; 2 = Flowering; 3 = Post-flowering; 4 = Dried Plants)

Fig 5.8. Changes in the concentration of Nitrogen in whole forbs throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.9. The Nitrogen Concentration (% Dry Weight) in Whole Forbs

Species	Pre-Flowering Oct to Dec		Flowering Plants Jan to Mar		Post-Flowering Apr to June		Dried Plants July to Sept	
	Mean SE	n	Mean SE	n	Mean SE	n	Mean SE	n
Evolvulus alsinoides	2.3 ± 0.2	2	1.9 ± 0.1	6	1.7 ± 0.3	3	1.4 ± -	1
Hermannia grisea	2.0 ± 0.1	10	1.8 ± 0.1	4	1.3 ± 0.2	5	- -	-
Indigofera macra	2.3 ± 0.1	6	2.2 ± 0.2	3	2.0 ± -	1	1.7 ± 0.0	2
Justicia flava	4.0 ± 0.1	2	2.9 ± 0.0	3	3.0 ± 0.1	2	- -	-
Oldenlandia herbacea	1.6 ± 0.3	2	1.1 ± 0.0	3	1.2 ± 0.1	2	- -	-
Pollichia campestris	2.5 ± 0.2	8	1.5 ± 0.3	2	1.4 ± 0.2	2	1.1 ± -	1
Sida [illegible]	2.4 ± 0.2	4	2.3 ± 0.1	7	1.8 ± 0.0	2	1.5 ± 0.2	3
Solanum panduraeforme	4.0 ± 0.2	8	2.5 ± 0.2	3	2.3 ± 0.1	4	2.1 ± 0.0	2
Tephrosia forbesii	2.4 ± 0.2	2	2.4 ± 0.4	2	1.4 ± 0.2	3	- -	-
Waltheria indica	1.9 ± 0.1	9	1.6 ± 0.2	3	1.5 ± 0.1	3	1.2 ± -	1



(1 = Pre-flowering; 2 = Flowering; 3 = Post-flowering; 4 = Dried Plants)

Fig 5.9. . Changes in the concentration of Phosphorus in whole forbs throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.10. The Phosphorus Concentration (mg / 100g) in Whole Forbs

Species	Pre- Flowering Oct to Dec			Flowering Plants Jan to Mar			Post- Flowering Apr to June			Dried Plants July to Sept		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
Evolvulus alsinoides	155.6	±17.7	2	152.3	±14.2	5	99.0	± -	1	103.0	±11.6	2
Hermannia grisea	130.4	±15.5	8	146.7	±39.0	2	139.0	± -	1	106.0	± -	1
Indigofera macra	124.0	± 5.8	5	158.5	±16.4	3	-	-	-	129.5	±52.5	2
Justicia flava	147.0	± -	1	167.1	±22.3	3	143.6	± 4.5	2	-	-	-
Oldenlandia herbacea	149.9	±47.1	2	132.5	± 1.2	2	64.3	±27.6	2	72.9	± -	1
Pollichia campestris	233.6	±45.6	7	125.2	±30.7	2	83.7	± 9.4	3	72.0	± -	1
Sida cordifolia	233.4	±44.2	4	224.1	±37.0	7	211.0	± -	1	347.5	±86.8	3
Solanum panduraeforme	316.9	±23.0	6	373.6	±82.7	2	215.0	±46.4	4	184.0	±55.0	2
Tephrosia forbesii	143.6	±25.1	2	140.5	±17.6	2	81.4	±12.4	2	-	-	-
Waltheria indica	119.7	±14.5	6	155.5	±19.8	3	194.5	±33.5	4	83.0	± 6.0	2

phosphorus were S. panduraeforme and S. cordifolia with 370-180 mg/100g, while O. herbacea contained only 150-60 mg/100g of phosphorus (Table 5.10.).

iii. Potassium

The potassium concentration of many forb species decreased as the plants aged (Fig 5.10.). P. campestris and J. flava were richest in potassium containing over 2600 mg/100g (Table 5.11.). Preflowering plants of S. panduraeforme were also rich in potassium. O. herbacea contained less than a quarter of the potassium concentration of these three forb species.

iv. Calcium

The concentration of calcium in whole forbs remained fairly stable throughout the year (Fig 5.11.). J. flava was exceedingly rich in calcium with 2000-3000 mg/100g (Table 5.12.). The second richest plant, contained only half this amount of calcium. O. herbacea and H. grisea contained only 400-800mg/100g.

v. Magnesium

The magnesium content of the forbs remained fairly constant, although a slight decline was evident for T. forbesii, P.campestris and J. flava plants as they aged (Fig 5.12). By far the richest species was J. flava with 870-720 mg/100g (Table 5.13.), while the next richest species, P. campestris, contained

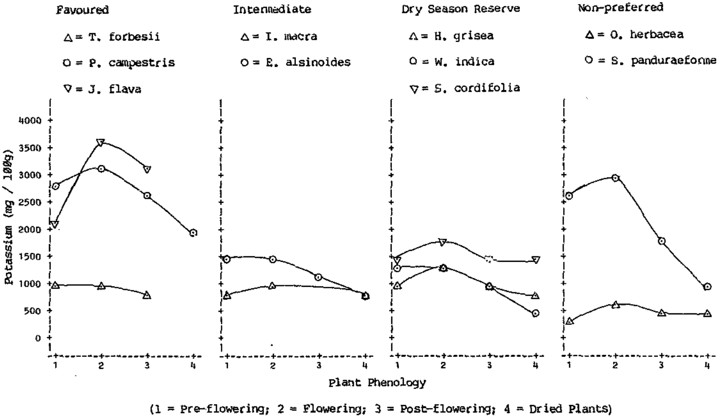


Fig 5.10. Changes in the concentration of Potassium in whole forbs throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.11. *The Potassium Concentration (mg / 100g) in Whole Forbs*

Species	Pre-Flowering Oct to Dec Mean	SE	n	Flowering Plants Jan to Mar Mean	SE	n	Post-Flowering Apr to June Mean	SE	n	Dried Plants July to Sept Mean	SE	n
Evolvulus alsinoides	1531.2	±117.3	2	1458.4	± 58.7	5	1239.0	± –	1	865.3	± 32.0	2
Hermannia grisea	1376.9	±107.8	8	1410.1	± 13.9	2	1054.0	± –	1	795.3	± –	1
Indigofera macra	797.9	± 41.4	5	1034.4	±186.7	3	–	± –	–	773.5	±358.5	2
Justicia flava	2161.0	± –	1	3633.3	±341.7	3	3230.4	± 62.7	2	–	–	–
Oldenlandia herbacea	331.8	± 71.0	2	628.2	± 5.7	2	458.6	± 49.2	2	498.1	± –	1
Pollichia campestris	2878.1	±106.7	7	3132.9	±110.6	2	2674.9	±305.5	3	2020.0	± –	1
Sida cordifolia	1521.5	± 59.8	4	1872.6	±101.5	7	1428.0	±247.1	2	1457.1	±147.8	3
Solanum panduraeforme	2640.2	±290.5	6	2936.8	±464.2	2	1893.8	±119.1	4	1032.0	± 60.0	2
Tephrosia forbesii	987.0	±160.1	2	990.0	±189.2	3	841.6	±152.5	2	–	–	-
Waltheria indica	1028.9	± 76.5	6	1260.7	±138.5	3	987.9	± 64.8	3	574.0	±190.0	2

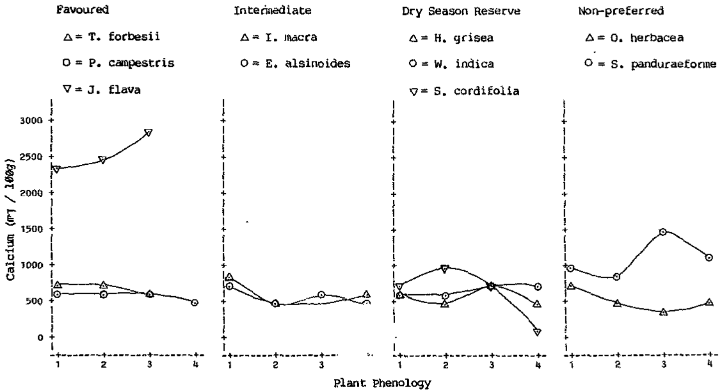
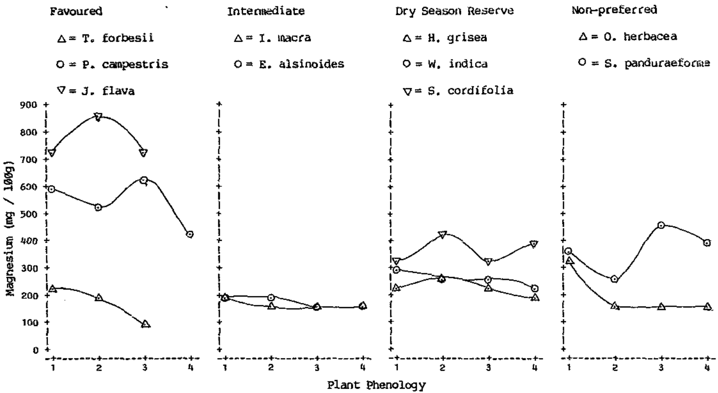


Fig 5.11. Changes in the concentration of Calcium in whole forbs throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.12. The Calcium Concentration (mg / 100g) in Whole Forbs

Species	Pre-Flowering Oct to Dec Mean ± SE	n	Flowering Plants Jan to Mar Mean ± SE	n	Post-Flowering Apr to June Mean ± SE	n	Dried Plants July to Sept Mean ± SE	n
Evolvulus alsinoides	725.3 ±199.4	2	533.4 ± 66.5	5	674.7 ± -	1	461.2 ± 28.7	2
Hermannia grisea	585.3 ± 29.3	8	490.5 ± 70.0	2	763.0 ± -	1	442.0 ± -	1
Indigofera macra	845.5 ± 87.5	5	452.8 ± 46.4	3	- + -	-	571.5 ±263.5	2
Justicia flava	2393.0 ± -	1	2502.4 ± 64.9	3	2873.0 ±458.0	2	- -	-
Oldenlandia herbacea	766.7 ±350.4	2	469.2 ± 45.4	2	421.3 ± 32.3	2	469.6 ± -	1
Icllichia campestris	590.8 ± 52.3	7	623.7 ±124.5	2	576.7 ± 33.8	?	512.0 ± -	1
Sida cordifolia	722.6 ± 67.0	4	981.4 ± 85.1	7	779.8 ±197.3	2	1077.4 ± 47.6	3
Solanum panduraeforme	1056.9 ± 88.4	6	822.0 ± 21.1	2	1545.5 ±130.4	4	1180.5 ±773.5	2
Tephrosia forbesii	757.6 ±164.9	2	689.2 ± 67.5	3	642.3 ± 390.3	2	- -	-
Waltheria indica	668.2 ± 42.4	6	658.9 ± 56.7	3	756.1 ± 73.4	4	717.5 ± 18.5	2



(1 = Pre-flowering; 2 = Flowering; 3 = Post-flowering; 4 = Dried Plants)

Fig 5.12. Changes in the concentration of Magnesium in whole forbs throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.13. The Magnesium Concentration (*mg / 100g*) in Whole Forbs

Species	Pre- Flowering Oct to Dec			Flowering Plants Jan to Mar			Post- Flowering Apr to June			Dried Plants July to Sept		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
Evolvulus alsinoides	209.8 ±	6.2	2	186.3 ±	16.1	5	183.8 ±	–	1	157.4 ±	1.5	2
Hermannia grisea	227.4 ±	13.2	8	257.2 ±	13.9	2	260.0 ±	–	1	198.0 ±	–	1
Indigofera macra	197.5 ±	8.3	5	179.7 ±	29.4	3	–	–	–	145.5 ±	10.5	2
Justicia flava	723.0 ±	–	1	868.8 ±	150.2	3	729.3 ±	123.7	2	–	–	–
Oldenlandia herbacea	322.2 ±	170.9	2	149.3 ±	20.0	2	171.4 ±	19.9	2	148.4 ±	–	1
Pollichia campestris	604.5 ±	28.2	7	525.6 ±	108.4	2	642.9 ±	87.8	3	428.0 ±	–	1
Sida cordifolia	327.8 ±	27.5	4	432.8 ±	20.8	7	322.6 ±	21.5	2	389.3 ±	31.4	3
Solanum panduraeforme	380.6 ±	34.7	5	265.9 ±	46.8	2	461.7 ±	77.6	4	389.0 ±	216.0	2
Tephrosia forbesii	219.9 ±	32.5	2	198.3 ±	98.1	3	102.7 ±	16.7	3	–	–	–
Waltheria indica	293.9 ±	24.1	6	267.0 ±	12.0	3	243.0 ±	7.5	3	240.5 ±	16.5	2

650-430 mg/100g. Least magnesium was found in T. forbesii, E. alsinoides and I. macra plants with little over 200 mg/100g.

vi. Sodium

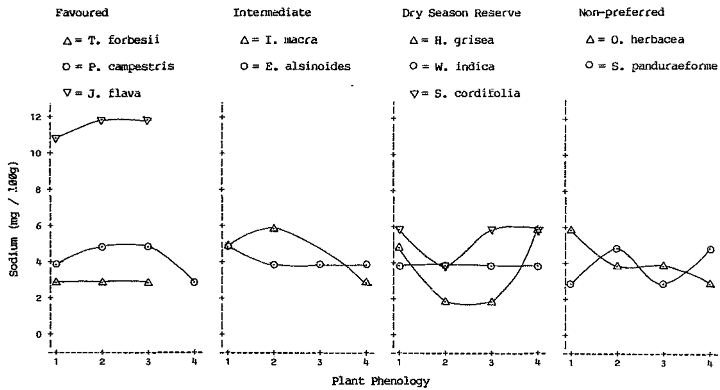
Sodium was scarce in forbs and showed no seasonal change (Fig 5.13.). J. flava contained most sodium with 12 mg/100g as opposed to 3 mg/100g in T. forbesii. (Table 5.14.).

iiv. Moisture

Several forb species contained over 70% water in the wet season and none contained less than 60% water (Table 5.15.). Generally there was a decrease in the moisture content of forb plants as they aged, but the stemmy, perennial species had a slightly lower moisture content in the immature phase than at maturity due to the fact that the new leaves grew on the previous years stems (Fig 5.14.). In the dry season most species contained around 45% moisture but E. alsinoides and O. herbacea plants dried up to contain only 26-32% water.

viii. Relationship between Nutrients

In forbs phosphorus was not correlated to the nitrogen content and was relatively independent of other minerals (Table 5.16.). Nitrogen tended to be positively correlated to sodium. Strong positive correlations existed between magnesium with calcium and potassium. Moisture was also correlated to potassium and magnesium

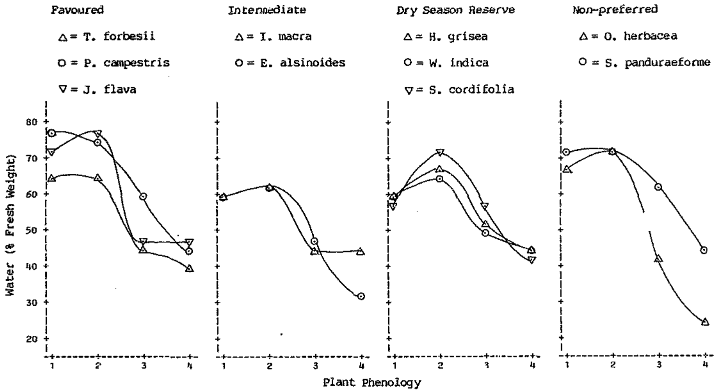


(1 = Pre-flowering; 2 = Flowering; 3 = Post-flowering; 4 = Dried Plants)

Fig 5.13. Changes in the concentration of Sodium in whole forbs throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.14. *The Sodium Concentration (mg / 100g) in Whole Forbs*

Species	Pre-Flowering Oct to Dec			Flowering Plants Jan to Mar			Post-Flowering Apr to June			Dried Plants July to Sept		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
Evolvulus alsinoides	5.0	± -	1	3.8	± 0.5	5	3.6	± -	1	4.4	± 1.3	2
Hermannia grisea	4.6	± 0.4	7	2.2	± 2.0	2	2.4	± -	1	5.7	± -	1
Indigofera macra	5.3	± 1.5	5	5.7	± 1.8	3	-	-	-	3.3	± 0.5	2
Justicia flava	11.2	± -	1	11.9	± 2.6	3	12.0	± 0.3	2	-	-	-
Oldenlandia herbacea	6.0	± 3.5	2	3.9	± 1.6	2	3.6	± 0.4	2	2.8	± -	1
Pollichia campestris	3.7	± 0.3	7	4.9	± 0.2	2	5.0	± 1.6	3	3.0	± -	1
Sida cordifolia	5.8	± 1.8	3	4.0	± 0.4	7	6.3	± -	1	6.3	± 1.3	3
Solanum panduraeforme	3.2	± 0.6	6	4.5	± 0.7	2	3.4	± 0.5	4	5.0	± -	1
Tephrosia forbesii	2.6	± 0.2	2	3.3	± 0.4	3	3.3	± 1.7	2	-	-	-
Waltheria indica	4.4	± 0.8	4	4.0	± 0.7	3	3.8	± 0.7	3	3.7	± 2.0	2



(1 = Pre-flowering; 2 = Flowering; 3 = Post-flowering; 4 = Dried Plants)

Fig 5.14. Changes in the concentration of Water in whole forbs throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.15. The Moisture Content (% Fresh Weight) of Whole Forbs

Species	Pre-Flowering Oct to Dec			Flowering Plants Jan to Mar			Post-Flowering Apr to June			Dried Plants July to Sept		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
Evolvulus alsinoides	60.0	± 3.0	2	61.9	± 2.6	9	47.5	±10.5	2	32.0	± 0.0	2
Hermannia grisea	60.9	± 3.9	15	68.5	± 1.2	6	53.1	± 2.2	7	44.0	±10.0	2
Indigofera macra	59.8	± 3.0	6	62.6	± 3.1	5	46.0	± –	1	44.3	± 4.8	3
Justicia flava	72.4	± 3.6	5	77.1	± 1.6	8	48.5	± 1.5	2	47.5	± 0.5	2
Oldenlandia herbacea	68.5	±11.5	2	73.4	± 1.9	5	42.0	± 4.0	2	26.0	±12.0	2
Pollichia campestris	77.6	± 1.4	14	74.3	± 1.0	4	61.0	± 2.2	5	45.5	± 0.5	2
Sida cordifolia	58.3	± 2.2	11	71.8	± 2.5	8	57.8	± 2.0	4	42.6	± 2.8	5
Solanum panduraeforme	73.0	± 2.0	12	72.4	± 2.5	5	63.5	± 4.8	4	44.5	±11.4	4
Tephrosia forbesii	65.5	± 2.1	4	66.0	± 2.9	5	44.3	± 5.1	4	41.0	± –	1
Waltheria indica	60.7	± 1.8	10	65.4	± 0.6	5	51.1	± 2.6	7	44.0	±11.9	3

Table 5.16. Intercorrelations Between the Nutrient Concentrations in Whole Forbs

i. Pre-flowering Plants (October to December)

	Nitrogen		Phosphorus		Potassium		Calcium		Magnesium		Sodium	
	r	n	r	n	r	n	r	n	r	n	r	n
Phosphorus	0.568	10										
Potassium	0.712*	10	0.733*	10								
Calcium	0.750*	10	-0.015	10	0.289	10						
Magnesium	0.611	10	0.311	10	0.023	10	0.690*	10				
Sodium	0.359	10	-0.280	10	0.023	10	0.839**	10	0.585	10		
Water	0.509	10	0.603	10	0.652*	10	0.275	10	0.708*	10	-0.014	10

ii. Flowering Plants (January to March)

	Nitrogen		Phosphorus		Potassium		Calcium		Magnesium		Sodium	
	r	n	r	n	r	n	r	n	r	n	r	n
Phosphorus	0.482	10										
Potassium	0.493	10	0.389	10								
Calcium	0.675*	10	0.120	10	0.692*	10						
Magnesium	0.481	10	-0.003	10	0.835**	10	0.892***	10				
Sodium	0.565	10	0.015	10	0.653*	10	0.904***	10	0.826**	10		
Water	0.136	10	0.205	10	0.672*	10	0.599	10	0.711*	10	0.492	10

iii. Post-flowering Plants (April to June)

	Nitrogen		Phosphorus		Potassium		Calcium		Magnesium		Sodium	
	r	n	r	n	r	n	r	n	r	n	r	n
Phosphorus	0.413	9										
Potassium	0.745*	9	0.155	9								
Calcium	0.965***	9	0.336	9	0.741*	9						
Magnesium	0.685*	9	0.197	9	0.967***	9	0.704*	9				
Sodium	0.791*	9	0.141	9	0.765*	9	0.823**	9	0.725*	9		
Water	0.182	10	0.565	9	0.518	9	0.145	9	0.586	9	-0.001	9

iv. Dried Plants (July to September)

	Nitrogen		Phosphorus		Potassium		Calcium		Magnesium		Sodium	
	r	n	r	n	r	n	r	n	r	n	r	n
Phosphorus	0.486	6										
Potassium	-0.267	6	0.302	8								
Calcium	0.697	6	0.766*	8	0.21.	8						
Magnesium	0.057	6	0.471	8	0.822*	8	0.648	8				
Sodium	0.494	6	0.748*	8	0.119	8	0.531	8	0.299	8		
Water	0.121	6	0.310	8	0.408	8	0.433	8	0.603	8	0.347	8

(Significance Levels : * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$)

in the growing season.

ix. Distribution of Nutrients between Forb Species

J. flava contained far higher concentrations of all nutrients except phosphorus than most other species. S. panduraeforme was also rich in nutrients, especially nitrogen, phosphorus and calcium. P. campestris was rich in potassium and magnesium, while S. cordifolia was rich in potassium and phosphorus.

The forb containing the least nutrients was O. herbacea. H. grisea was low in calcium and T. forbesii contained relatively little magnesium and sodium.

c. *A Comparison of Nutrient Concentrations* in Woody Plant Leaves and Whole Forbs

Woody plants showed a rather more clear cut seasonal change in the quantities of nitrogen, phosphorus, potassium and calcium in the foliage than was observed for forbs. Forbs did not appear to accumulate calcium in their tissues as the plants aged, even though this was noticeable for woody plants.

The two forb species J. flava and S. panduraeforme had higher nutrient levels in their tissues than were found in any woody plants. On average forbs tended to contain higher levels of potassium and magnesium than woody plants, but levels of nitrogen, phosphorus, calcium and sodium were not significantly different

Table 5.17. Comparison between the Nutrient Concentrations in Mature Leaves of Woody Plants and in Whole Forbs

Nutrient	Woody Plant Leaves				Whole Forbs					
	Mean	SE	Max	Min	Mean	SE	Max	Min	n	t
Nitrogen (%)	2.0 ±	0.1	3.0 -	1.4	2.0 ±	0.2	2.9 -	1.1	24	0.447
Phosphorus (mg/100g)	131.5 ±	9.3	193.1 -	90.9	177.6 ±	23.4	324.1 -	125.3	24	1.831
Potassium (mg/100g)	1012.0 ±	107.5	1861.0 -	450.8	1835.7 ±	326.6	3633.3 -	628.2	24	2.396*
Calcium (mg/100g)	711.7 ±	67.5	1223.3 -	427.1	822.4 ±	194.0	2502.4 -	452.8	24	0.539
Magnesium (mg/100g)	257.9 ±	24.1	383.3 -	99.2	333.1 ±	7.1	868.8 -	149.3	24	2.989*
Sodium (mg/100g)	3.5 ±	0.3	5.6 -	1.3	4.8 ±	0.9	11.6 -	2.2	24	1.463

(* Significantly Different : $P < 0.05$)

between the leaves of woody plants and whole forbs including stem tissue (Table 5.17.). Thus forbs leaves are on average probably more nutrient rich than woody plant leaves. The variation between individual plant species however is greater than that between growth forms.

The ratio of minerals was similar in woody plants and forbs for all minerals except for potassium which made up a greater proportion of the mineral content of forbs. In all plants potassium was the most common mineral and sodium was scarce.

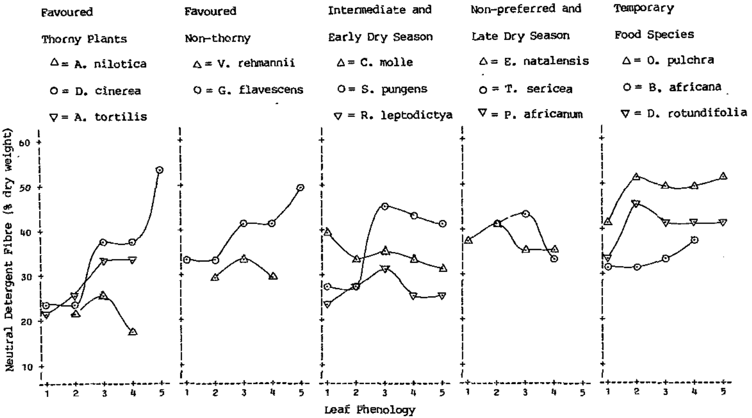
2. Fibre

a. Woody Plants

i. Neutral Detergent Fibre (NDF)

The neutral detergent fibre content of the foliage of woody plants was lowest in the new leaves then increased once the leaves had attained full size (Fig 5.15.).

The most fibrous mature leaves were those of O. pulchra. Almost half the dry weight of these leaves was due to fibre. Leaves of S. pungens and T. sericea also contained over 40% fibre. The Acacia species and the two aromatic species, R. leptodictya and V. rehmannii had the least fibrous leaves (Table 5.18.).



(1 = New leaves; 2 = Young leaves; 3 = Mature leaves; 4 = Old leaves; 5 = Dried leaves)

Fig 5.15. Changes in the concentration of Neutral Detergent Fibre in the leaves of woody plants throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.18. The Neutral Detergent Fibre Concentration (% Dry Weight) in Woody Plant Leaves and Stems

Species	New leaves Spring flush Mean SE	n	Young leaves Oct to Dec Mean SE	n	Mature leaves Jan to Mar Mean SE	n	Old leaves Apr to June Mean SE	n	Dried leaves July to Sept Mean SE	n	Soft stems Oct to Dec Mean SE	n	Hard stems Jan to Sept Mean SE	n
Acacia nilotica	– –	–	22.5 ± 5.7	2	26.9 ± 6.9	2	17.5 ± –	1	– –	–	49.7 ± –	1	– –	–
Acacia tortilis	22.7 ± –	1	25.9 ± –	1	33.8 ± 0.9	2	34.1 ± 1.2	2	– –	–	– –	–	– –	–
Burkea africana	32.4 ± –	1	32.4 ± –	1	34.9 ± 0.4	2	39.0 ± 0.7	2	– –	–	– –	–	– –	–
Combretum molle	40.2 ± –	1	34.4 ± 1.2	5	35.2 ± 1.1	5	33.4 ± 1.0	2	31.6 ± –	1	49.6 ± 4.3	3	56.7 ± 0.6	2
Dichrostachys cinerea	24.0 ± –	1	24.0 ± –	1	39.0 ± –	1	39.0 ± –	1	53.9 ± –	1	61.6 ± –	1	61.6 ± –	1
Dombeya rotundifolia	34.3 ± –	1	46.6 ± 0.6	2	41.0 ± 1.1	5	42.4 ± 1.3	4	42.7 ± –	1	36.7 ± –	1	45.0 ± 4.5	2
Euclea natalensis	38.3 ± –	1	41.1 ± 1.9	3	36.5 ± –	1	36.5 ± –	1	– –	–	45.1 ± 2.2	4	48.5 ± 1.1	4
Grewia flavescens	33.1 ± –	1	34.8 ± 0.7	3	41.3 ± 1.6	4	42.3 ± 0.5	4	50.3 ± –	1	– –	–	57.9 ± 1.0	2
Ochna pulchra	41.2 ± –	1	52.6 ± 2.6	3	50.9 ± 2.0	6	50.7 ± 2.7	3	52.4 ± –	1	50.2 ± –	1	57.7 ± 2.6	3
Peltophorum africanum	– –	–	– –	–	– –	–	– –	–	– –	–	– –	–	– –	–
Rhus leptodictya	24.6 ± –	1	27.5 ± 1.0	4	31.2 ± 3.8	3	26.0 ± 1.4	4	25.7 ± –	1	28.7 ± –	1	41.4 ± 2.9	4
Strychnos pungens	28.2 ± –	1	28.2 ± –	1	46.8 ± 1.3	4	44.8 ± 2.2	5	42.1 ± 0.5	2	33.0 ± –	1	52.4 ± 9.1	3
Terminalia sericea	– –	–	41.8 ± 0.1	3	44.9 ± –	1	33.8 ± –	1	– –	–	– –	–	– –	–
Vitex rehmannii	– –	–	29.4 ± –	1	33.8 ± 0.5	2	30.3 ± 1.4	2	– –	–	53.3 ± –	1	51.6 ± –	1

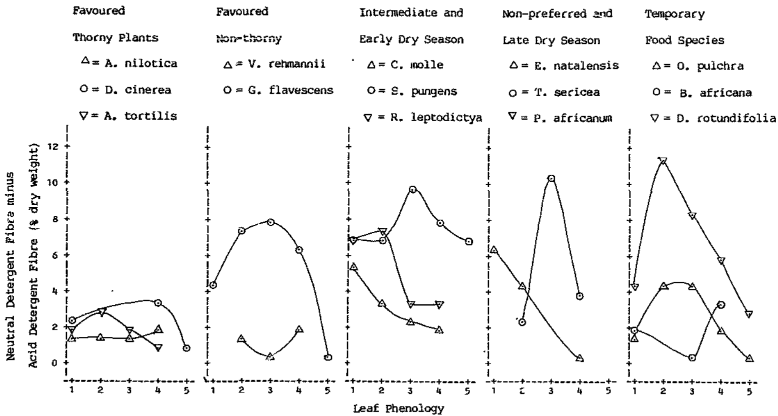
The leaves of most species were significantly less fibrous than the stem tissue. The least fibrous new, soft stems were those of D. rotundifolia and R. leptodictya. These were no more fibrous than the leaves with only 28-36% fibre. Even after hardening the stems of these two species were the least fibrous. D. cinerea, C. molle and O. pulchra stems always contained over 50% fibre, but the tough mature leaves of O. pulchra were no less fibrous than the stems.

The foliage of P. africanum could not be analysed for fibre as it formed a thick mucilaginous slime with the neutral solution, so stopping the extraction process.

ii. Neutral Detergent Fibre minus Acid Detergent Fibre (NDF - ADF)

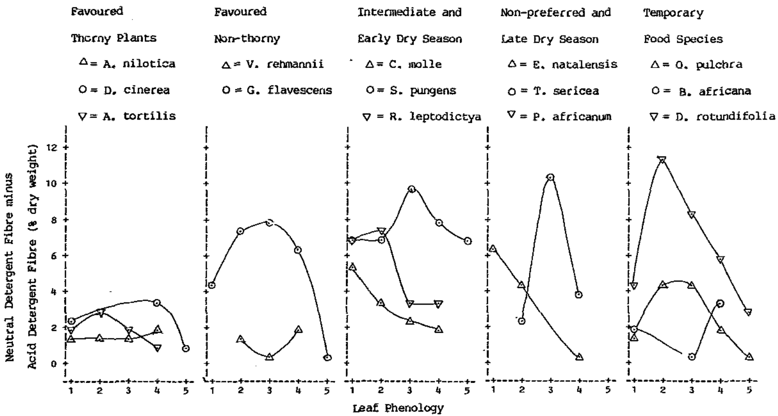
Using the detergent fibre method of analysis the difference between the NDF and ADF fractions is a rough measure of the hemicellulose content. Taking into consideration that up to a quarter of the hemicellulose may be lost in this procedure, hemicellulose is still a minor constituent of the total fibre content of woody plants.

The NDF - ADF content of woody plant leaves appeared to reach a peak in the young or mature leaves then decrease as the leaves began to senesce (Fig 5.16.). This change however was not significant due to the wide range of NDF - ADF values recorded within individual species. The leaves of D. rotundifolia and G.



(1 = New leaves; 2 = Young leaves; 3 = Mature leaves; 4 = Old leaves; 5 = Dried leaves)

Fig 5.16. Changes in the concentration of Neutral Detergent Fibre minus Acid Detergent Fibre in the leaves of woody plants throughout the year. Plants grouped according to their acceptance to browsing ungulates.



(1 = New leaves; 2 = Young leaves; 3 = Mature leaves; 4 = Old leaves; 5 = Dried leaves)

Fig5.16. Changes in the concentration of Neutral Detergent Fibre minus Acid Detergent Fibre in the leaves of woody plants throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.19. The Neutral Detergent Fibre minus Acid Detergent Fibre Concentration (% Dry Weight) in Woody Plant Leaves and Stems

Species	New leaves Spring flush Mean ± SE	n	Young leaves Oct to Dec Mean ± SE	n	Mature leaves Jan to Mar Mean ± SE	n	Old leaves Apr to June Mean ± SE	n	Dried leaves July to Sept Mean ± SE	n	Soft stems Oct to Dec Mean ± SE	n	Hard stems Jan to Sept Mean ± SE	n
Acacia nilotica	1.3 ± –	1	1.3 ± 0.7	2	1.7 ± 0.9	2	1.9 ± –	1	– –	–	6.1 ± –	1	– –	–
Acacia tortilis	2.0 ± –	1	2.9 ± –	1	1.9 ± 0.2	2	0.9 ± 0.4	2	– –	–	– –	–	– –	–
Burkea africana	1.9 ± –	1	– –	–	0.7 ± 0.6	2	3.3 ± 0.4	2	– –	–	– –	–	– –	–
Combretum molle	5.5 ± –	1	3.3 ± 0.4	3	2.4 ± 0.6	5	2.1 ± 0.9	2	– –	–	8.7 ± 1.2	3	6.1 ± 1.0	2
Dichrostachys cinerea	2.7 ± –	1	– –	–	– –	–	3.4 ± –	1	1.2 ± –	–	5.7 ± –	1	5.4 ± –	1
Dombeya rotundifolia	4.3 ± –	1	11.5 ± 0.4	2	8.7 ± 2.0	5	6.0 ± 0.5	4	3.2 ± –	1	3.2 ± –	1	4.0 ± 0.2	2
Euclea natalensis	6.4 ± –	1	4.7 ± 2.2	3	– ± –	–	0.3 ± –	1	– –	–	3.1 ± 0.6	4	1.6 ± 0.8	4
Grewia flavescens	4.4 ± –	1	7.6 ± 0.9	3	7.9 ± 0.7	4	6.7 ± 0.6	4	0.7 ± –	1	– –	–	3.0 ± 1.3	2
Ochna pulchra	1.3 ± –	1	4.3 ± 1.1	3	4.5 ± 1.7	6	1.8 ± 0.9	3	0.3 ± –	1	5.3 ± –	1	7.9 ± 3.1	3
Peltophorum africanum	– –	–	– –	–	– –	–	– –	–	– –	–	– –	–	– –	–
Rhus leptodictya	6.9 ± –	1	7.3 ± 0.5	4	3.3 ± 0.5	3	3.3 ± 1.8	4	– –	–	2.0 ± –	1	3.6 ± 0.8	4
Strychnos pungens	7.1 ± –	1	7.1 ± –	1	9.8 ± 0.7	4	8.2 ± 1.8	5	7.2 ± 0.2	2	9.0 ± –	1	10.9 ± 3.2	3
Terminalia sericea	– –	–	2.4 ± 0.8	3	10.7 ± –	1	4.2 ± –	1	– –	–	– –	–	– –	–
Vitex rehmannii	– –	1	1.5 ± –	1	0.6 ± 0.1	2	1.8 ± 0.8	2	– –	–	10.9 ± –	1	6.5 ± –	1

flavescens were richest in this fraction which constituted less than 10% of the dry weight (Table 5.19.). The leaves of V. rehmannii and Acacia species contained only 3% NDF - ADF.

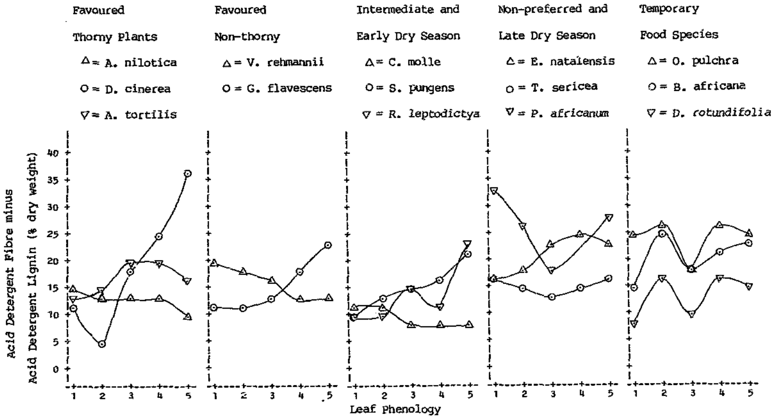
Stems were generally richer in this fraction than leaves, except for D. rotundifolia, G. flavescens and R. leptodictya in which the pattern was reversed.

iii. Acid Detergent Fibre minus Acid Detergent Lignin (ADF - ADL)

Acid Detergent Fibre consists mainly of two fractions, cellulose and lignin. Due to their differing digestibilities these fractions have been considered separately.

The ADF - ADL approximates to the cellulose content of plants. The ADF - ADL concentration increased in the leaves of A. nilotica, D. cinerea, G. flavescens and the evergreen species as they aged. For B. africana and O. pulchra the main increase in this fibre component came once the leaves achieved full size. The remaining species showed little change in the ADF - ADL contents of the leaves throughout the season (Fig 5.17.). Leaves of O. pulchra and P. africanum contained over 25% ADF - ADL. B. africana and E. natalensis were also rich in this fibre (Table 5.20). A. nilotica, C. molle and R. leptodictya contained less than 15% of ADF - ADL.

Within species the ADF - ADL content of leaves and stems was similar. The soft stems of B. africana and G. flavescens were rich



(1 = New leaves; 2 = Young leaves; 3 = Mature leaves; 4 = Old leaves; 5 = Dried leaves)

Fig 5.17. Changes in the concentration of Acid Detergent Fibre minus Acid Detergent Lignin in the leaves of woody plants throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.20. The Acid Detergent Fibre minus Acid Detergent Lignin Concentration (% Dry Weight) in Woody Plant Leaves and Stems

Species	New leaves			Young leaves			Mature leaves			Old leaves			Dried leaves			Soft stems			Hard stems		
	Spring flush			Oct to Dec			Jan to Mar			Apr to June			July to Sept			Oct to Dec			Jan to Sept		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
Acacia nilotica	15.7	± -	1	13.5	± 6.9	2	13.3	± 4.0	3	12.8	± 2.1	4	10.5	± -	1	13.8	± -	1	-	-	-
Acacia tortilis	12.5	± -	1	14.7	± 3.3	2	19.6	± 1.3	3	20.0	± 1.3	5	17.3	± -	1	-	-	-	-	-	-
Burkea africana	14.8	± -	1	25.7	± -	1	17.7	± 3.8	2	20.9	± 2.5	3	23.0	± -	1	21.7	± -	1	-	-	-
Combretum molle	12.3	± -	1	12.1	± 2.9	5	8.1	± 0.5	5	7.9	± 0.8	3	8.8	± -	1	7.7	± 1.3	3	14.0	± 2.0	2
Dichrostachys cinerea	12.2	± -	1	5.8	± -	1	19.0	± 1.8	3	24.4	± 2.2	3	36.9	± -	1	17.2	± -	1	-	-	-
Dombeya rotundifolia	9.0	± -	1	16.7	± 9.1	2	9.9	± 2.5	5	17.0	± 2.1	4	14.4	± -	1	11.8	± -	1	16.3	± 0.5	2
Euclea natalensis	16.7	± -	1	18.3	± 2.5	6	23.8	± 1.7	5	22.4	± 1.3	4	22.8	± 0.2	2	16.6	± 1.[illegible]	7	12.[illegible]	[illegible] 2.7	5
Grewia flavescens	12.4	± -	1	12.3	± 2.6	3	13.7	± 1.5	4	18.8	± 1.6	4	23.6	± -	1	25.3	± -	1	17.3	± 0.8	2
Ochna pulchra	24.7	± 5.8	2	27.4	± 1.8	4	19.8	± 3.8	6	26.2	± 0.4	3	25.3	± -	1	14.4	± -	1	26.2	± 0.6	3
Peltophorum africanum	32.9	±15.1	3	26.6	± 1.4	3	17.6	± 1.7	4	25.2	± 2.2	4	27.5	± -	1	17.7	± -	1	22.8	± 1.7	2
Rhus leptodictya	10.4	± -	1	10.4	± 0.4	4	14.4	± 4.5	3	11.6	± 0.8	5	22.5	± -	1	11.4	± -	1	14.9	± 1.4	4
Strychnos pungens	[illegible].2	± -	1	32.6	± -	1	14.4	± 3.5	3	17.3	± 1.2	5	21.4	± 5.3	2	8.1	± -	1	14.7	± 1.9	4
Terminalia sericea	16.8	± 5.7	2	14.3	± 0.7	5	12.8	± -	1	15.1	± 1.2	3	16.7	± -	1	-	-	-	31.5	± -	1
Vitex rehmannii	19.6	± -	1	37.9	± 1.9	4	16.6	± 2.6	4	13.1	± 1.3	3	13.9	± -	1	12.4	± -	1	13.4	± -	1

in this fibre while those of C. molle and S. pungens contained only 8%. The hardened stems of T. sericea, O. pulchra and P. africanum contained the most ADF - ADL and E. natalensis and V. rehmannii shoots contained the least.

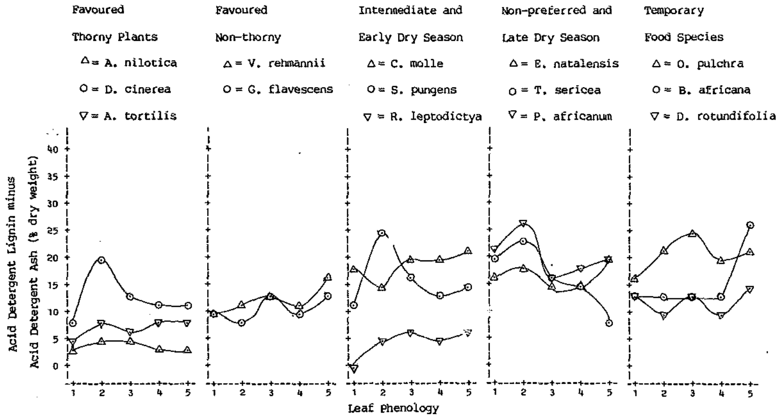
iv. Acid Detergent *Lignin minus* Acid Detergent Ash (ADL - Ash)

The ADL content of the leaves was fairly constant through out the year (Fig 5.18.). Leaves of O. pulchra, P. africanum and T. sericea contained in excess of 20% ADL, while the leaves of R. leptodictya and the Acacia species contained only half this quantity (Table 5.21.).

Unlike the leaves, the stems did become increasingly lignified at maturity. Generally stems contained more ADL than the leaves, except in the case of O. pulchra, T. sericea and the two evergreen species, where both leaves and stems contained similar amounts of ADL on a dry weight basis. The stems of D. rotundifolia and R. leptodictya were relatively low in ADL as were the leaves. The stems of D. cinerea, G. flavescens and C. molle were the most lignified.

v. Relationship between Fibre Constituents

Neutral detergent fibre was most closely correlated to ADL in all but the dried leaves, The converse pattern was true of ADF - ADL which only correlated with NDF in the dry season (Table 5.22.). ADL and ADF - ADL concentrations correlated only in immature



(1 = New leaves; 2 = Young leaves; 3 = Mature leaves; 4 = Old leaves; 5 = Dried leaves)

Fig 5.18. Changes in the concentration of Acid Detergent lignin minus Acid Detergent Ash in the leaves of woody plants throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.21. The Acid Detergent Lignin minus Acid Detergent Ash Concentration (% Dry Weight) in Woody Plant Leaves and Stems

Species	New leaves Spring flush		Young leaves Oct to Dec		Mature leaves Jan to Mar		Old leaves Apr to June		Dried leaves July to Sept		Soft stems Oct to Dec		Hard stems Jan to Sept	
	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n
Acacia nilotica	4.5 ± -	1	4.4 ± 3.0	2	5.8 ± 1.3	2	3.9 ± 1.4	3	2.5 ± -	1	25.7 ± -	1	- -	-
Acacia tortilis	2.9 ± -	1	7.5 ± 1.3	2	7.2 ± 1.4	3	8.4 ± 0.4	5	9.1 ± -	1	- -	-	- -	-
Burkea africana	13.4 ± -	1	13.4 ± -	1	14.0 ± 2.2	2	13.7 ± 1.1	3	26.6 ± 7.3	2	18.4 ± -	1	- -	-
Combretum molle	17.7 ± -	1	15.6 ± 2.7	5	10.3 ± 0.9	5	20.0 ± 2.3	3	21.0 ± -	1	26.2 ± 2.9	3	32.4 ± 0.1	2
Dichrostachys cinerea	9.1 ± 4.5	2	20.3 ± -	1	13.8 ± 0.9	3	11.1 ± 0.6	3	10.9 ± -	1	35.2 ± -	1	- -	-
Dombeya rotundifolia	13.7 ± -	1	10.5 ± 8.4	2	13.9 ± 1.4	5	9.8 ± 1.5	4	14.6 ± -	1	12.1 ± -	1	17.8 ± 3.9	2
Euclea natalensis	16.2 ± -	1	18.1 ± 1.8	6	14.0 ± 1.2	5	14.3 ± 1.5	4	20.7 ± 1.8	2	21.5 ± 1.0	7	25.7 ± 3.0	5
Grewia flavescens	9.3 ± -	1	8.5 ± 2.2	3	13.2 ± 0.8	4	9.8 ± 1.7	4	13.8 ± -	1	20.2 ± -	1	33.0 ± 0.1	2
Ochna pulchra	16.3 ± 0.1	2	22.1 ± 3.1	4	25.3 ± 3.9	6	20.4 ± 1.9	3	21.4 ± -	1	22.9 ± -	1	20.1 ± 1.9	3
Peltophorum africanum	21.4 ± 6.8	3	27.1 ± 0.8	3	16.6 ± 1.0	4	17.8 ± 2.4	4	20.1 ± -	1	19.7 ± -	1	23.9 ± 1.7	3
Rhus leptodictya	0.6 ± -	1	4.2 ± 1.4	4	6.7 ± 3.9	3	4.0 ± 2.0	5	14.7 ± -	1	9.5 ± -	1	10.3 ± 2.8	4
Strychnos pungens	10.9 ± -	1	25.3 ± -	1	16.5 ± 3.6	3	13.9 ± 1.6	5	7.0 ± 3.1	2	12.7 ± -	1	33.7 ± 1.6	4
Terminalia sericea	20.5 ± 11.9	2	23.1 ± 1.0	5	16.1 ± -	1	15.4 ± 1.5	3	6.3 ± -	1	- -	-	14.9 ± -	1
Vitex rehmannii	10.8 ± -	1	12.4 ± 1.9	4	13.8 ± 1.0	4	11.7 ± 0.7	3	16.7 ± -	1	23.4 ± -	1	25.4 ± -	1

foliage. Concentrations of NDF - ADF were fairly independant of the other fibre fractions. All forms of fibre accumulated in the stems as the plants aged, but for the leaves the major accumulation of fibre was when they achieved full size, there after little or no increase in fibre concentration was evident for many of the species.

The main difference in the fibre contents of leaves and stems was in the greater proportion of NDF and ADL in stem tissue, Average concentrations of the other fibre components did not differ significantly between leaves and stems (Table 5.23.). Since ADL is but a component of NDF it seems that it is ADL which is the greatest distinguishing component between leaf and stem tissue.

vi. Distribution of Fibre Components between Plant Species

The ADF fraction accounted for most of the fibre in woody plant foliage, with NDF - ADF making up only a small proportion of the total fibre content. The most fibrous leaves were those of O. pulchra, T. sericea, S. pungens and P. africanum. Acacia leaves contained least fibre, but the thorny stems were fairly fibrous.

The species with the most fibrous stems were O. pulchra, G. flavescens, C. molle and D. cinerea. The stems of O. pulchra were comprised mainly of ADF - ADL while those of D. cinerea were comparatively rich in ADL. D. rotundifolia and R. leptodictya stems were low in all forms of fibre.

Table 5.22. Intercorrelations Between the Fibre Concentrations in Woody Plant Leaves

i. New Leaves

	NDF		NDF - ADF		ADF - ADL	
	r	n	r	n	r	n
NDF - ADF	0.074	13				
ADF - ADL	0.421	13	-0.584*	13		
ADL	0913***	13	-0.033	13	0.552*	14

ii. Young Leaves (October to December)

	NDF		NDF - ADF		ADF - ADL	
	r	n	r	n	r	n
NDF - ADF	0.370	13				
ADF - ADL	0.337	13	0.091	13		
ADL	0.394	13	-0.092	13	0.540*	14

iii. Mature Leaves (January to March)

	NDF		NDF - ADF		ADF - ADL	
	r	n	r	n	r	n
NDF - ADF	0.706**	13				
ADF - ADL	0.014	13	-0.303	13		
ADL	0.778**	13	0.272	13	0.001	14

iv. Old Leaves (April to June)

	NDF		NDF - ADF		ADF - ADL	
	r	n	r	n	r	n
NDF - ADF	0.408	13				
ADF - ADL	0.655*	13	-0.057	13		
ADL	0.616*	13	-0.075	13	0.306	14

v. Dried Leaves (July to September)

	NDF		NDF - ADF		ADF - ADL	
	r	n	r	n	r	n
NDF - ADF	-0.161	13				
ADF - ADL	0.714**	13	-0.162	13		
ADL	0.273	13	-0.295	13	0.185	14

(Significance Levels : * P < 0.05; ** P < 0.01; *** P < 0.001)

Table 5.23. Comparison between the Fibre Concentrations (% Dry Weight) in Mature Leaves and the Hardened Stems of Woody Plants

Nutrient	Woody Plant Leaves		Hardened Stems			
	Mean SE	Max Min	Mean SE	Max Min	n	t
NDF	38.7 ± 2.0	46.8 - 26.9	51.5 ± 2.4	61.1 - 41.4	22	4.370***
NDF - ADF	4.7 ± 1.1	10.7 - 0.6	5.6 ± 0.9	10.9 - 7.6	21	0.636
ADF - ADL	15.7 ± 1.1	23.8 - 8.1	18.3 ± 2.0	31.5 - 12.0	24	1.129
ADL	14.1 ± 1.4	25.3 - 5.8	23.5 ± 1.9	33.7 - 14.9	24	4.008***

(* Significantly Different : $P < 0.05$)

b. Forbs

i. Neutral Detergent Fibre (NDF)

Whole forbs became increasingly fibrous as the seasons progressed (Fig 5.19.). Many forbs contained in excess of 40% NDF (Table 5.24.). The most fibrous species, P. campestris, O. herbacea, I. macra and T. forbesii, contained between 40% and 60% fibre. The least fibrous plant J. flava has fairly soft green stems and contained only half this amount of fibre.

ii. Neutral Detergent Fibre minus Acid Detergent Fibre (NDF - ADF)

This fraction was a minor component of the total fibre content of most forb species and showed little seasonal change in concentration within the plants (Fig 5.20.). S. cordifolia and P. campestris contained 14% of NDF - ADF while for J. flava and W. indica this fraction comprised less than 4% of the dry mass of the plants. Most other forb species contained between 6 and 8% of NDF - ADF (Table 5.25.).

iii. Acid Detergent Fibre minus Acid Detergent Lignin (ADF - ADL)

Concentrations of ADF - ADL showed only a slight seasonal increase for most forb species and none at all for J. flava and I. macra (Fig 5.21.). P. campestris, W. indica and T. forbesii were comparatively rich in ADF - ADL, but for J. flava, S. cordifolia and E. alsinoides this fraction accounted for only 10% of the dry

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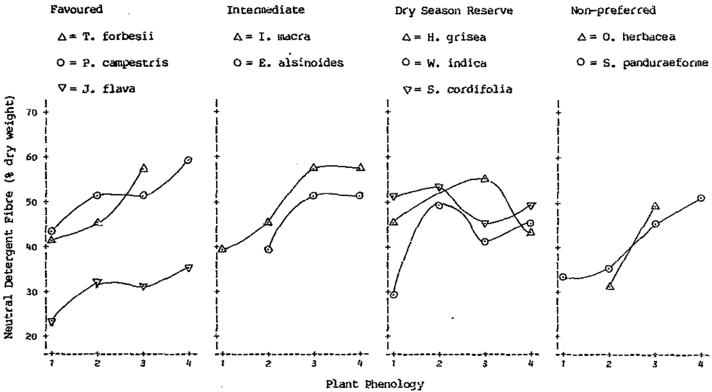
iii. Acid Detergent Fibre minus Acid Detergent Lignin (ADF - ADL)

Concentrations of ADF - ADL showed only a slight seasonal increase for most forb species and none at all for J. flava and I. macra (Fig 5.21.). P. campestris, W. indica and T. forbesii were comparatively rich in ADF - ADL, but for J. flava, S. cordifolia and E. alsinoides this fraction accounted for only 10% of the dry

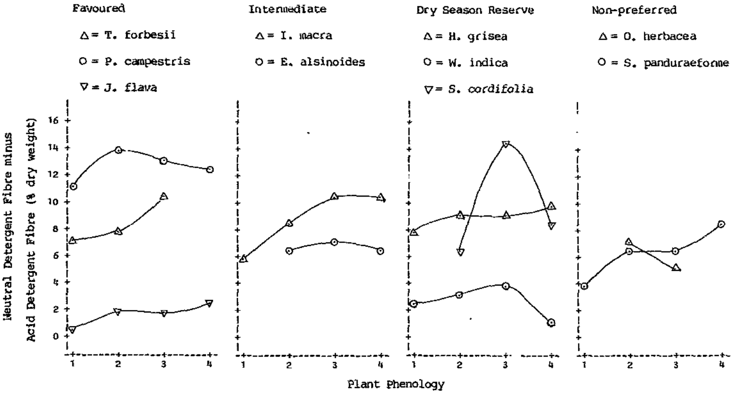


(1 = Pre-flowering; 2 = Flowering; 3 = Post-flowering; 4 = Dried Plants)

Fig 5.19. Changes in the concentration of Neutral Detergent Fibre in whole forbs throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.24. The Neutral Detergent Fibre Concentration (% Dry Weight) in Whole Forbs

Species	Pre-Flowering Oct to Dec			Flowering Plants Jan to Mar			Post-Flowering Apr to June			Dried Plants July to Sept		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
Evolvulus alsinoides	–	–	–	41.1	± 2.0	4	51.8	± 0.9	2	51.1	± –	1
Hermannia grisea	46.6	± 2.3	4	46.0	± 2.3	3	55.8	± 3.9	4	44.6	± –	1
Indigofera macra	40.9	± 4.0	3	50.9	± 3.1	3	57.1	± –	1	58.5	± 2.6	2
Justicia flava	24.1	± –	1	31.9	± 2.6	4	31.8	± 3.4	2	35.1	± –	1
Oldenlandia herbacea	–	–	–	52.5	± 0.8	2	49.4	± 8.3	3	–	–	–
Pollichia campestris	44.1	± 2.8	6	53.7	± 1.2	4	52.4	± –	1	60.7	± –	1
Sida cordifolia	51.7	± 3.9	2	36.9	± 3.3	4	47.0	± –	1	50.4	± 3.2	2
Solanum panduraeforme	34.2	± 1.7	4	45.5	± 4.4	4	45.6	± –	1	51.7	± 5.5	2
Tephrosia forbesii	41.2	± –	1	49.8	± 2.2	3	57.2	± 0.7	2	–	–	–
Waltheria indica	31.0	± 1.2	4	37.7	± 3.1	3	41.1	± 2.0	2	45.2	± –	1



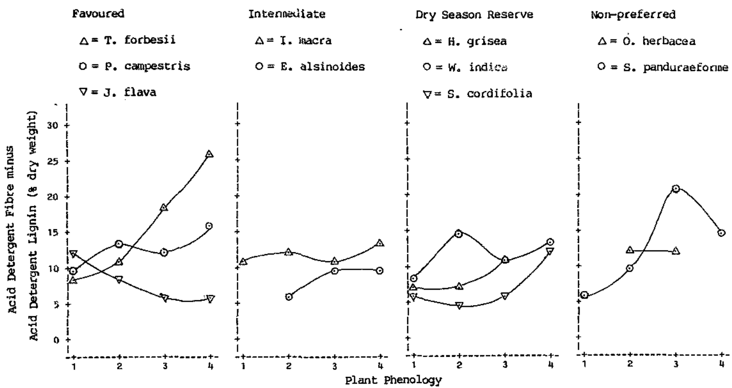
(1 = Pre-flowering; 2 = Flowering; 3 = Post-flowering; 4 = Dried Plants)

Fig 5.20 Changes in the concentration of Neutral Detergent Fibre minus Acid Detergent Fibre in whole forbs *throughout the year. Plants grouped according to their acceptance to browsing ungulates.*

Table 5.25.

The Neutral Detergent Fibre minus Acid Detergent Fibre Concentration (% Dry Weight) in Whole forbs

Species	Pre-Flowering Oct to Dec Mean ± SE	n	Flowering Plants Jan to Mar Mean ± SE	n	Post-Flowering Apr to June Mean ± SE	n	Dried Plants July to Sept Mean ± SE	n
Evolvulus alsinoides	- -	-	6.6 ± 0.9	4	7.3 ± 0.3	2	6.7 ± -	1
Hermannia grisea	8.1 ± 0.7	4	9.0 ± 0.6	3	9.5 ± 0.4	4	9.7 ± -	1
Indigofera macra	6.3 ± 1.9	3	8.6 ± 1.0	3	10.6 ± -	1	10.6 ± 1.2	2
Justicia flava	0.6 ± -	1	2.1 ± 0.8	4	2.1 ± 0.9	2	2.9 ± -	1
Oldenlandia herbacea	- -	-	7.4 ± 0.2	2	5.2 ± 1.2	3	- -	-
Pollichia campestris	11.6 ± 1.0	6	13.9 ± 0.7	4	13.4 ± -	1	12.7 ± -	1
Sida cordifolia	16.7 ± 3.9	2	6.6 ± 0.6	4	14.4 ± -	1	8.4 ± 1.7	2
Solanum panduraeforme	4.1 ± 0.7	4	6.7 ± 1.9	4	6.8 ± 2.6	1	8.5 ± -	1
Tephrosia forbesii	7.3 ± -	1	7.8 ± 0.9	3	10.4 ± 0.1	2	- -	-
Waltheria indica	2.9 ± 0.2	4	3.0 ± 0.9	3	3.9 ± 0.2	2	1.0 ± -	1



(1 = Pre-flowering; 2 = Flowering; 3 = Post-flowering; 4 = Dried Plants)

Fig 5.21. Changes in the concentration of Acid Detergent Fibre minus Acid Detergent Lignin in whole forbs throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.26.

The Acid Detergent Fibre minus Acid Detergent Lignin Concentration (% Dry Weight) in Whole Forbs

Species	Pre- Flowering Oct to Dec		Flowering Plants Jan to Mar		Post- Flowering Apr to June		Dried Plants July to Sept	
	Mean SE	n	Mean SE	n	Mean SE	n	Mean SE	n
Evolvulus alsinoides	– –	–	6.0 ± 1.2	4	10.5 ± –	1	10.6 ± –	1
Hermannia grisea	7.9 ± 0.5	4	7.5 ± 3.5	3	11.0 ± 3.7	4	– –	–
Indigofera macra	10.7 ± 0.7	3	12.7 ± 0.9	3	11.0 ± –	1	13.4 ± 0.5	2
Justicia flava	12.8 ± –	1	8.8 ± 0.3	4	6.1 ± 0.3	2	5.8 ± –	1
Oldenlandia herbacea	– –	–	13.0 ± –	1	13.0 ± 3.6	3	– –	–
Pollichia campestris	10.2 ± 0.9	6	13.9 ± 0.5	4	12.9 ± –	1	15.8 ± –	1
Sida cordifolia	6.3 ± 2.5	2	5.6 ± 0.5	6	6.8 ± –	1	12.1 ± 1.2	3
Solanum panduraeforme	6.4 ± 0.4	4	9.7 ± 1.2	4	21.7 ± –	1	15.6 ± 4.9	4
Tephrosia forbesii	9.1 ± –	1	11.5 ± 0.7	3	19.0 ± 3.8	3	26.5 ± –	1
Waltheria indica	8.9 ± 1.3	4	15.5 ± 4.9	3	11.6 ± 1.4	3	13.3 ± 5.3	2

mass of the plants (Table 5.26.).

iv. Acid Detergent Lignin minus Acid Detergent Ash (ADL - Ash)

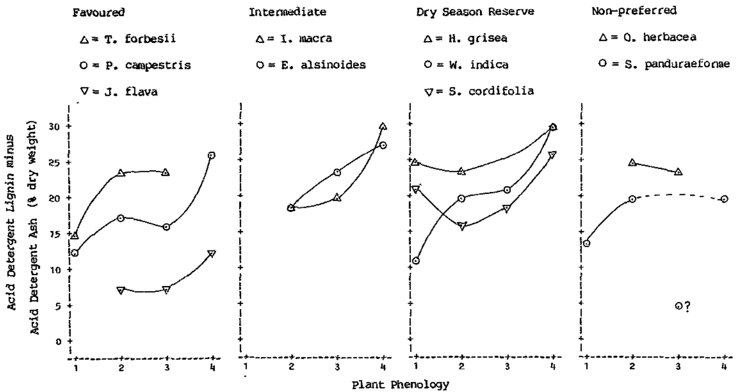
The concentration of ADL showed a seasonal increase in concentration for all forb species (Fig 5.22.). Both O. herbacea and H. grisea were relatively highly lignified containing over 23% ADL (Table 5.27.). Most other forbs contained in excess of 15% ADL once they were matured. J. flava contained the least ADL of all the plants analysed, containing only 8% of this fraction.

v. Relationship between Fibre Constituents

Neutral detergent fibre was significantly correlated to both the ADL and the NDF - ADF fractions at all times, but only to ADF - ADL in dried plants (Table 5.28.). The three sub-fractions of NDF showed no significant intercorrelations.

vi. Distribution of Fibre Components between Forb Species

J. flava contained very little fibre of any type. O. herbacea and H. grisea were the most lignified of the forb species analysed and S. panduraeforme and T. forbesii were rich in ADF - ADL. Concentrations of NDF and and its component ADL showed an accumulation as the tissues aged, but concentrations of ADF - ADL and NDF - ADF remained fairly constant.



(1 = Pre-flowering; 2 = Flowering; 3 = Post-flowering; 4 = Dried Plants)

Fig 5.22. Changes in the concentration of Acid Detergent Lignin minus Acid Detergent Ash in whole forbs throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.27.

The Acid Detergent Lignin minus Acid Detergent Ash Concentration (% Dry Weight) in Whole Forbs

Species	Pre-Flowering Oct to Dec			Flowering Plants Jan to Mar			Post-Flowering Apr to June			Dried Plants July to Sept		
	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
Evolvulus alsinoides	-	-	-	18.2 ±	2.2	4	24.3 ±	-	1	28.0 ±	-	1
Hermannia grisea	24.5 ±	2.4	4	23.5 ±	4.3	3	31.2 ±	1.0	4	29.9 ±	-	1
Indigofera macra	-	-	-	18.7 ±	4.8	2	20.4 ±	4.4	3	29.8 ±	5.8	2
Justicia flava	-	-	-	7.5 ±	1.4	2	8.1 ±	4.3	2	12.4 ±	-	1
Oldenlandia herbacea	-	-	-	25.5 ±	-	1	23.8 ±	5.8	3	-	-	-
Pollichia campestris	12.1 ±	1.4	5	17.3 ±	1.7	4	16.0 ±	-	1	25.7 ±	-	1
Sida cordifolia	21.8 ±	5.2	2	16.5 ±	2.0	6	18.7 ±	-	1	25.9 ±	2.6	3
Solanum panduraeforme	13.3 ±	1.1	4	20.1 ±	2.4	4	5.1 ±	-	1	20.4 ±	5.4	3
Tephrosia forbesii	15.5 ±	-	1	24.0 ±	0.5	3	23.4 ±	3.3	3	-	-	-
Waltheria indica	11.1 ±	1.7	3	19.9 ±	1.0	2	21.8 ±	1.7	3	29.9 ±	6.8	2

Table 5.28. Intercorrelations Between the Fibre Concentrations in Whole Forbs

i. Pre-flowering Plants (October to December)

	NDF		NDF - ADF		ADF - ADL	
	r	n	r	n	r	n
NDF - ADF	0.821**	10				
ADF - ADL	-0.151	10	-0.354	10		
ADL	0.874***	10	-0.534	10	-0.143	10

ii. Flowering Plants (January to March)

	NDF		NDF - ADF		ADF - ADL	
		n	r	n	r	n
NDF - ADF	[illegible]	10				
ADF - ADL	[illegible]	10	0.148	10		
ADL	[illegible]	10	0.382	10	0.259	10

iii. Post-flowering Plants (April to June)

	NDF		NDF - ADF		ADF - ADL	
	r	n	r	n	r	n
NDF - ADF	0.667*	10				
ADF - ADL	0.358	10	0.038	10		
ADL	0.625*	10	0.234	10	-0.176	10

iv. Dried Plants (July to September)

	NDF		NDF - ADF		ADF - ADL	
	r	n	r	n	r	n
NDF - ADF	0.876***	10				
ADF - ADL	0.738**	10	0.582	10		
ADL	0.716*	10	0.359	10	0.386	10

(Significance Levels : * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$)

c. A Comparison between Fibre Contents of Woody Plant Leaves and Whole Forbs

On average, forbs contained a slightly higher proportion of all fibre fractions than did woody plant leaves, due to the inclusion of stem tissue of the forbs. The differences however were only significant for ADL (Table 5.29.). This is partly because ADL is a major component of stem tissue in both woody plants and forbs but also the ratio of ADL to ADF - ADL of forbs was higher at 1.8 than in either woody plant leaves (0.9) or stems (1.3).

3. The Relationship between Nutrient and Fibre Contents of Plants

a. Woody Plants

As the leaves and stems of woody plants aged the amount of fibre increased and hence the relative quantity of cell sap containing most of the nutrients decreased. Only concentrations of calcium, which is partly associated with the cell walls, increased as the foliage matured.

The nitrogen concentration in the leaves was negatively correlated to ADL contents in all but the dried leaves (Table 5.30.). The relationship between the other nutrients and fibre components other than NDF - ADF were generally negative but failed to reach significance at the 95% confidence limits. The correlations between NDF - ADF and nutrients were often around

Table 5.29. Comparison between the Fibre Concentrations (% Dry Weight) in Mature Leaves of Woody Plants and in Whole Forbs

Nutrient	Woody Plant Leaves		Whole Forbs			
	Mean SE	Max Min	Mean SE	Max Min	n	t
NDF	38.7 ± 2.0	46.8 – 26.9	44.6 ± 2.3	53.7 – 31.9	22	2.003
NDF – ADF	4.7 ± 1.1	10.7 – 0.6	7.2 ± 1.0	13.9 – 2.1	21	2.000
ADF – ADL	15.7 ± 1.1	23.8 – 8.1	10.4 ± 1.1	13.9 – 5.6	24	3.421
ADL	14.1 ± 1.4	25.3 – 5.8	19.1 ± 1.6	25.5 – 7.5	24	2.357*

(* Significantly Different : $P < 0.05$)

Table 5.30. Intercorrelations Between the Nutrient and Fibre Concentrations in Woody Plant Leaves

i. New Leaves

	NDF		NDF - ADF		ADF - ADL		ADL	
	r	n	r	n	r	n	r	n
Nitrogen	-0.490	13	-0.560*	13	-0.326	14	-0.556*	14
Phosphorus	-0.222	12	-0.467	12	-0.117	13	-0.486	13
Potassium	-0.302	12	0.138	12	-0.086	13	-0.366	13
Calcium	-0.002	12	0.165	12	-0.338	13	-0.212	13
Magnesium	-0.199	12	0.008	12	-0.162	13	-0.279	13
Sodium	-0.461	12	-0.127	12	-0.323	13	-0.620*	13
Water	0.238	13	-0.067	13	-0.126	14	0.036	14

ii. Young Leaves (October to December)

	NDF		NDF - ADF		ADF - ADL		ADL	
	r	n	r	n	r	n	r	n
Nitrogen	-0.370	13	0.31[illegible]	13	-0.445	14	-0.652*	14
Phosphorus	-0.153	13	0.288	13	-0.414	14	-0.491	14
Potassium	-0.326	13	0.362	13	-0.656*	14	-0.426	14
Calcium	0.003	13	0.489	13	-0.692**	14	-0.460	14
Magnesium	-0.241	13	0.310	13	-0.589*	14	-0.088	14
Sodium	0.128	13	0.306	13	0.238	14	-0.155	14
Water	0.226	13	0.529	13	0.190	14	0.008	14

iii. Mature Leaves (January to March)

	NDF		NDF - ADF		ADF - ADL		ADL	
	r	n	r	n	r	n	r	n
Nitrogen	-0.314	13	-0.167	13	-0.122	14	-0.616*	14
Phosphorus	-0.064	13	0.219	13	-0.216	14	-0.351	14
Potassium	-0.443	13	-0.082	13	-0.274	14	-0.529	14
Calcium	-0.269	13	0.071	13	-0.296	14	-0.447	14
Magnesium	0.055	13	0.199	13	-0.418	14	0.047	14
Sodium	-0.291	13	-0.046	13	-0.248	14	-0.354	14
Water	0.004	13	0.196	13	-0.312	14	-0.306	14

Table 5.30. Continued. . .

iv. Old Leaves (April to June)

	NDF		NDF - ADF		ADF - ADL		ADL	
	r	n	r	n	r	n	r	n
Nitrogen	-0.140	13	0.029	13	0.069	14	-0.647*	14
Phosphorus	-0.273	13	0.133	13	-0.319	14	-0.575*	14
Potassium	-0.303	13	0.142	13	-0.408	14	-0.683**	14
Calcium	-0.345	13	0.114	13	-0.567*	14	-0.608*	14
Magnesium	-0.132	13	0.019	13	-0.314	14	0.032	14
Sodium	-0.098	13	0.184	13	-0.142	14	-0.468	14
Water	-0.269	13	0.278	13	-0.267	14	-0.291	14

iiv. Dried Leaves (July to September)

	NDF		NDF - ADF		ADF - ADL		ADL	
	r	n	r	n	r	n	r	n
Nitrogen	-0.042	13	-0.034	13	0.176	14	-0.515	14
Phosphorus	-0.178	13	0.098	13	0.119	14	-0.414	14
Potassium	-0.013	13	0.034	13	-0.017	14	-0.196	14
Calcium	-0.121	13	-0.158	13	-0.455	14	-0.354	14
Magnesium	-0.165	13	0.031	13	-0.173	14	0.221	14
Sodium	-0.449	11	-0.243	11	-0.573	11	-0.471	11
Water	-0.321	13	0.388	13	-0.241	14	-0.400	14

(Significance Levels : * P < 0.05; ** P < 0.01; *** P < 0.001)

zero or slightly positive rather than negative as for the other fibre fractions.

The armed species tended to be of high nitrogen and low fibre content (Fig 5.23.). The ratio between the NDF and crude protein content of the leaves of the Acacia species was between 1 and 2.5 while leaves of the third armed species D. cinerea and of G. flavescens and R. leptodictya also had a low fibre to protein ratio.

Leaves of O. pulchra initially had a low proportion of fibre but by the late dry season the leaves contained eight times as much NDF as protein. Many species contained four times as much fibre as protein by the late dry season.

b. Forbs

As with woody plants the build up of cell wall components in forbs gradually diluted the quantity of cell sap and hence most nutrients in the tissues. The nitrogen concentration in forbs was significantly negatively correlated to the NDF and ADL contents in the pre-flowering and post-flowering phase forbs but fell to just below the 95% confidence limits in the flowering phase plants (Table 5.31.). The relationship between nitrogen and NDF - ADF or ADF - ADL contents of forbs was negative but not significant. The relationship between all the minerals, except phosphorus, with ADL was negative and reached significance in the flowering phase. Correlations between minerals and NDF were similar to those with

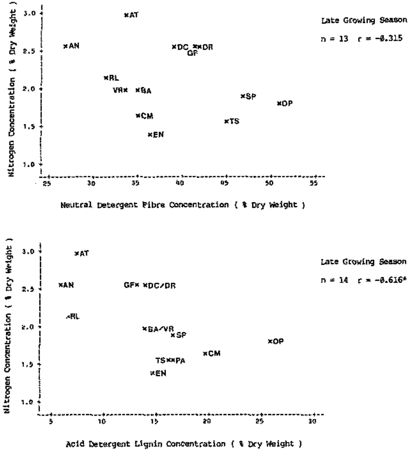


Fig 5.23. The Relationship between Nitrogen and Fibre Concentrations in Mature Leaves of Woody Plants.

Table 5.31. Intercorrelations Between the Nutrient and Fibre Concentrations in Whole Forbs

i. Pre-flowering Plants (October to December)

	NDF		NDF - ADF		ADF - ADL		ADL	
	r	n	r	n	r	n	r	n
Nitrogen	-0.665*	10	-0.399	10	-0.038	10	-0.650*	10
Phosphorus	0.031	10	0.274	10	-0.430	10	-0.187	10
Potassium	-0.363	10	0.019	10	-0.430	10	-0.583	10
Calcium	-0.697*	10	-0.574	10	0.453	10	-0.564	10
Magnesium	-0.450	10	-0.182	10	0.460	10	-0.636*	10
Sodium	-0.380	10	-0.325	10	0.530	10	-0.223	10
Water	-0.156	10	-0.108	10	0.331	10	-0.398	10

ii. *Flowering Plants (January to March)*

	NDF		NDF - ADF		ADF - ADL		ADL	
	r	n	r	n	r	n	r	n
Nitrogen	-0.522	10	-0.420	10	-0.448	10	-0.602	10
Phosphorus	-0.201	10	-0.195	10	-0.281	10	-0.090	10
Potassium	-0.357	10	-0.034	10	-0.165	10	-0.758*	10
Calcium	-0.696*	10	-0.578	10	-0.247	10	-0.844**	10
Magnesium	-0.548	10	-0.240	10	-0.155	10	-0.880***	10
Sodium	-0.492	10	-0.458	10	-0.012	10	-0.870**	10
Water	-0.136	10	0.009	10	-0.052	10	-0.389	10

iii. Post-flowering Plants (April to June)

	NDF		NDF - ADF		ADF - ADL		ADL	
	r	n	r	n	r	n	r	n
Nitrogen	-0.675*	10	-0.428	10	-0.197	10	-0.785**	10
Phosphorus	-0.470	9	-0.045	9	-0.060	9	-0.419	9
Potassium	-0.563	9	-0.064	9	-0.263	9	-0.734*	9
Calcium	-0.800**	9	-0.537	9	-0.232	9	-0.714	9
Magnesium	-0.792*	9	-0.090	9	-0.254	9	-0.744*	9
Sodium	[illegible]*	10	-0.299	9	-0.596	9	-0.575	9
Water	[illegible]	10	-0.276	10	0.166	10	-0.510	10

iv. *Dried Plants* (July to September)

	NDF		NDF - ADF		ADF - ADL		ADL	
	r	n	r	n	r	n	r	n
Nitrogen	-0.046	6	0.166	6	0.345	6	-0.606	6
Phosphorus	-0.157	8	0.146	8	-0.101	8	-0.262	8
Potassium	0.562	8	0.682	8	0.451	8	-0.261	8
Calcium	-0.321	8	-0.056	8	0.371	8	-0.581	8
Magnesium	0.171	8	0.364	8	0.626	8	-0.526	8
Sodium	-0.169	8	0.085	8	-0.418	8	0.027	8
Water	-0.083	10	0.137	10	-0.044	10	-0.217	10

(Significance Levels : * P < 0.05; ** P < 0.01; *** P < 0.001)

ADL. Again The NDF - ADF and ADF - ADL contents of forbs were not significantly correlated to the mineral contents but the relationship tended to be negative.

The ratio of NDF to crude protein was very low in J. flava ranging from 1-2. S. panduraeforme was also relatively rich in protein and low in fibre. In contrast O. herbacea contained five times as much fibre as protein before flowering and as for other forbs fibre accumulated as the season progressed.

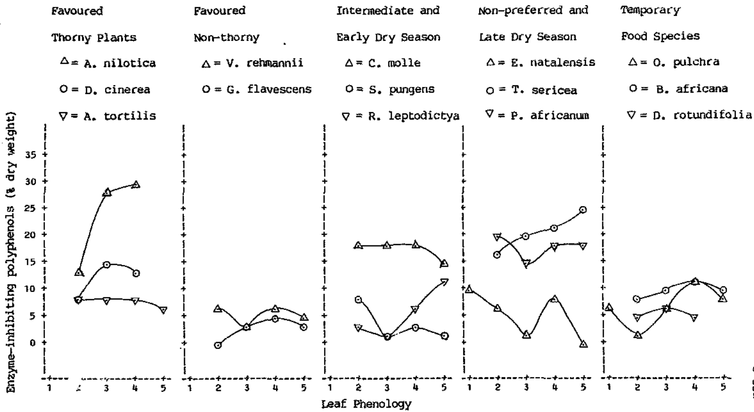
The fibre to protein ratio of S. cordifolia plants was higher for immature plants than in the reproductive phases. This was because the new leaves sprouted on a thick fibrous perennial stem.

4. Plant Secondary Compounds

a. Woody Plants

i. Enzyme-inhibiting Polyphenols

The enzyme-inhibiting polyphenol content of woody plant leaves was generally highest in the mature tissues (Fig 5.24). Immature leaves showed slightly lower polyphenol levels than mature leaves for all species except the three evergreen species and V. rehmannii. A lowering of polyphenol levels in senescent leaves was evident for all species except T.sericea.



(1 = New leaves; 2 = Young leaves; 3 = Mature leaves; 4 = Old leaves; 5 = Dried leaves)

Fig 5.24. Changes in the concentration of Enzyme-inhibiting Polyhenols in the leaves of woody plants throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.32. Concentrations of Total Polyphenols (% Dry Weight) in Composite Samples of Leaves of Woody Plant Species. Assayed by the Jerumanis Method.

Species	New leaves	Young leaves	Mature leaves	Old leaves	Dead leaves
Acacia nilotica	-	13.4	28.1	30.6	-
Acacia tortilis	-	7.5	8.5	8.7	6.6
Burkea africana	-	7.8	10.4	11.8	9.2
Combretum molle	-	18.0	17.6	18.4	14.9
Dichrostachys cinerea	-	8.5	15.8	13.5	-
Dombeya rotundifolia	-	4.8	6.5	4.2	-
Euclea natalensis	9.4	7.4	1.7	8.0	0.7
Grewia flavescens	-	0.5	4.1	4.7	3.4
Ochna pulchra	7.1	2.4	6.4	10.9	7.6
Peltophorum africanum	-	19.9	15.6	19.1	17.8
Rhus leptodictya	-	3.5	1.0	6.3	11.0
Strychnos pungens	-	7.6	1.6	3.8	1.3
Terminalia sericea	-	16.3	19.3	22.4	25.5
Vitex rehmannii	-	6.4	3.6	6.0	4.7

Concentrations of enzyme-inhibiting polyphenols in the leaves of woody plants ranged from less than 1% to 30% dry weight (Table 5.32.). A. nilotica was particularly rich in polyphenols which constituted about 30% of the dry weight of mature leaves. T. sericea contained 15-25% polyphenols and C. molle and P. africanum 15-20%. The majority of other plants contained around 10% polyphenols. G. flavescens, V. rehmannii and D. rotundifolia contained the least polyphenols and concentrations in immature G. flavescens leaves were negligible. The levels of polyphenols in E. natalensis varied greatly between samples. This may be due to chemical polymorphism within the population or to some interference with the analysis as all samples were composite samples taken from several plants. No confidence limits are available on these data but all samples are composite samples of about 10 individuals of each species.

ii. Condensed tannins

The condensed tannin (proanthocyanidin) content of mature woody plant leaves ranged from 0% to 12.5% dry weight relative to a Sorghum III tannin standard (Table 5.33.). Condensed tannins were absent from A. nilotica, S. pungens and V. rehmannii foliage. O. pulchra and T. sericea contained over 10% condensed tannins and D. rotundifolia, E. natalensis and B. africana contained more than 5% condensed tannins.

Table 5.33. Concentrations of Condensed Tannins (% Dry Weight) in the Mature of Leaves of Woody Plant Species. Assayed by the Bate-Smith Proanthocyanidin Method.

Species	Mature leaves			
	Mean		SE	n
Acacia nilotica	0.0	±	0.0	8
Acacia tortilis	3.0	±	0.2	8
Burkea africana	5.8	±	0.9	6
Combretum molle	1.0	±	0.1	8
Dichrostachys cinerea	3.5	±	0.2	8
Dombeya rotundifolia	8.8	±	0.8	10
Euclea natalensis	8.3	±	0.7	10
Grewia flavescens	3.0	±	0.3	8
Ochna pulchra	11.0	±	0.5	11
Peltophorum africanum	2.8	±	0.2	8
Rhus leptodictya	1.5	±	0.1	11
Strychnos pungens	0.0	±	0.0	7
Terminalia sericea	12.3	±	0.8	10
Vitex rehmannii	0.0	±	0.0	9

(n = Number of replicates of the same sample)

iii. Alkaloids

Alkaloids were relatively scarce in woody plant leaves (Table 5.34.). S. pungens and V. rehmannii were the only woody plants giving a consistant reaction with Mayer's reagent indicating the presence of alkaloids. The immature leaves of D. rotundifolia and T. sericea and mature green leaves of D. cinerea, O. pulchra and P. africanum also showed weak, positive responses to Mayer's and Dragendorff's reagents.

iv. Cyanogenic Glycosides

Cyanogenic glycosides were absent from the woody plant foliage tested.

v. Saponins

Newly emerged woody plant leaves contained little saponin (Table 5.35.). TLC on extract of mature leaves indicated that several plants contained saponins, but this technique also identifies some terpenes. TLC tests were confirmed by the foam test specific to saponins. Alcoholic extracts of B. africana, T. sericea and P. africanum foamed vigorously when shaken with water. O. pulchra and C. molle produced less foam and E. natalensis, D. rotundifolia, D. cinerea and A. tortilis only p[illegible] in film of foam. No saponins were detected in G. fl[illegible] S. pungens leaves at any time.

Table 5.34. The Presence of Alkaloids in the Leaves of Woody Plants, Detected by the *Formation of a Precipitate with Meyers* Reagent

Species	New leaves	Young leaves	Mature leaves	Old leaves	Dead leaves
Acacia nilotica	Ø	Ø	Ø	Ø	Ø
Acacia tortilis	Ø	Ø	Ø	Ø	Ø
Burkea africana	Ø	Ø	Ø	Ø	Ø
Combretum molle	Ø	Ø	Ø	Ø	Ø
Dichrostachys cinerea	Ø	Ø	+	+	Ø
Dombeya rotundifolia	++	Ø	Ø	Ø	Ø
Euclea natalensis	Ø	Ø	(+)	Ø	Ø
Grewia flavescens	Ø	Ø	Ø	(+)	Ø
Ochna pulchra	Ø	Ø	+	Ø	Ø
Peltophorum africanum	Ø	+	+	(+)	Ø
Rhus leptodictya	Ø	Ø	Ø	Ø	Ø
Strychnos pungens	Ø	(+)	++	+	++
Terminalia sericea	++	+	(+)	Ø	Ø
Vitex rehmannii	+	(	-	++	+

Meyers reagent
+++ = strong precipitation
++ = precipitation
+ = slight precipitation
(+) = clouding
Ø = no reaction

Table 5.35. The Presence of Saponins in the Leaves of Woody Plants. Assayed by Thin Layer Chromatography and the Foam Test.

Species	New leaves		Young lvs	Mature leaves		Old lvs	Dead lvs
	TLC	Foam	TLC	TLC	Foam	TLC	TLC
Acacia nilotica	Ø	Ø	-	+	+	Ø	Ø
Acacia tortilis	Ø	Ø	+	+	Ø	+	+
Burkea africana	Ø	Ø	Ø	+	+++	+	+
Combretum molle	Ø	Ø	Ø	+	++	+	+
Dichrostachys cinerea	Ø	Ø	+	+	+	+	+
Dombeya rotundifolia	Ø	Ø	+	+	+	+	+
Euclea natalensis	Ø	Ø	Ø	+	Ø	+	+
Grewia flavescens	Ø	Ø	Ø	Ø	Ø	Ø	Ø
Ochna pulchra	+	Ø	+	+	++	+	+
Peltophorum africanum	+	Ø	+	+	+++	+	+
Rhus leptodictya	Ø	Ø	+	+	+++	Ø	Ø
Strychnos punc[illegible]	+	Ø	Ø	Ø	Ø	Ø	+
Terminalia sericea	Ø	Ø	Ø	+	+++	+	+
Vitex rehmannii	Ø	Ø	Ø	+	++	-	Ø

TLC + = present

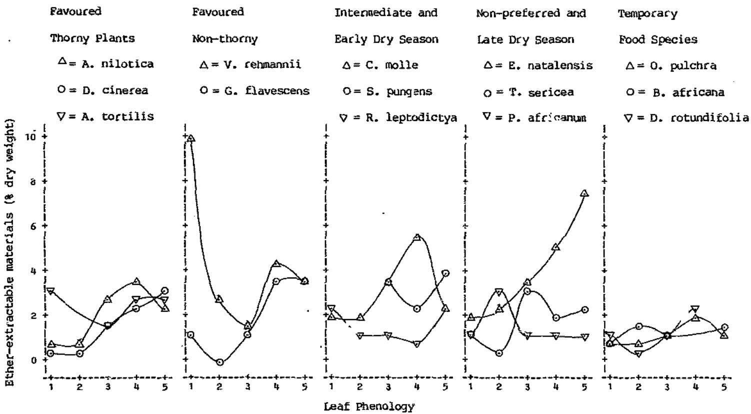
Ø = absent

Foaming +++ = 1 to 2 cm of pe[illegible]tant foam

++ = Ø.5 to 1 cm of persistant foam

\+ = slight but persistant foaming

Ø = no foaming



(1 = New leaves; 2 = Young leaves; 3 = Mature leaves; 4 = Old leaves; 5 = Dried leaves)

Fig 5.25. Changes in the concentration of Ether-extractable materials in the leaves of woody plants throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.36. Concentrations of Ether-extractable Materials (% Dry Weight) in Composite Samples of Leaves of Woody Plant Species.

Species	New leaves	Young leaves	Mature leaves	Old leaves	Dried leaves	Fallen leaves
Acacia nilotica	0.7	0.7	2.7	3.7	2.6	3.5
Acacia tortilis	3.2	-	1.6	2.7	2.7	3.5
Burkea africana	0.6	1.8	1.3	-	1.5	1.3
Combretum molle	1.9	1.9	3.4	5.6	2.6	2.6
Dichrostachys cinerea	0.5	0.4	1.5	2.6	3.1	2.0
Dombeya rotundifolia	1.0	0.4	1.3	2.4	-	1.3
Euclea natalensis	1.9	2.0	3.4	5.3	7.8	3.9
Grewia flavescens	1.3	0.2	1.3	3.4	3.6	0.7
Ochna pulchra	0.7	0.9	1.0	2.0	1.3	0.8
Peltophorum africanum	1.0	3.0	1.0	1.0	1.2	1.8
Rhus leptodictya	2.6	1.3	3.7	0.8	2.3	2.8
Strychnos pungens	-	-	3.0	2.3	4.0	5.2
Terminalia sericea	1.0	0.4	1.7	2.0	2.5	2.6
Vitex rehmannii	9.9	2.7	3.5	4.6	3.4	5.2

vi. Monoterpenes and Sesquiterpene Lactones

These "essential oils" were present in the leaves of all woody plants tested, and in all seasons. The most aromatic species were V. rehmannii and R. leptodictya. Monoterpenes are characteristically pungent or aromatic.

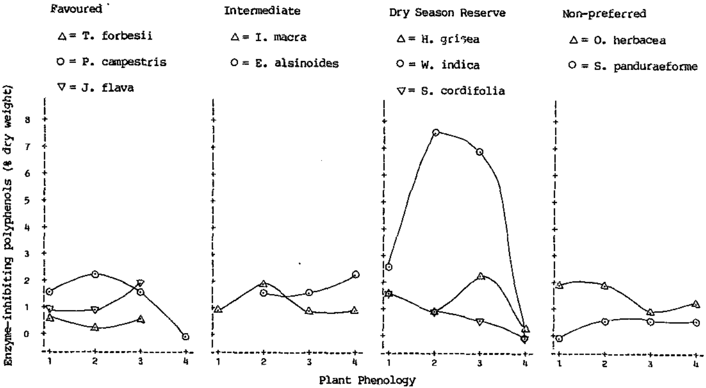
vii. Ether-extractable Compounds

The woody plant leaves tested generally contained between 1% and 6% ether-extractable materials (Table 5.36.). The highly aromatic, sticky, new foliage of V. rehmannii was the exception with 10% ether-extract. This species, C. molle, and the evergreens E. natalensis and S. pungens were richest in ether-extract. The concentration of ether-extractable compounds tended to increase as the leaves aged, this being particularly noticeable for E. natalensis, G. flavescens and the armed species (Fig 5.25.). B. africana, D. rotundifolia, O. pulchra and T. sericea contained least ether-extract containing less than 2% at all times and showed no seasonal increase in concentration.

b) Forbs

i. Enzyme-inhibiting Polyphenols

The concentrations of polyphenols in forbs were very low (Table 5.36.). The highest levels were found in mature W. indica plants



(1 = Pre-flowering; 2 = Flowering; 3 = Post-flowering; 4 = Dried Plants)

Fig 5.26. Changes in the concentration of Enzyme-inhibiting polyphenols in whole forbs throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.37. Concentrations of Total Polyphenols (% dry Weight) in Composite Samples of Whole Forbs. Assayed by the Jerumanis Method.

Species	Pre-Flowering Oct - Dec	Flowering Plants Jan - Mar	Post-Flowering Apr - Jun	Dried Plants Jul - Sept
Evolvulus alsinoides	-	1.7	1.6	2.2
Hermannia grisea	1.8	1.1	2.4	0.2
Indigofera macra	0.9	2.0	1.1	1.1
Justicia flava	1.1	1.0	2.0	-
Oldenlandia herbacea	2.1	2.1	1.1	1.2
Pollichia campestris	1.7	2.3	1.5	0.0
Sida cordifolia	1.5	1.1	0.5	0.0
Solanum panduraeforme	0.0	0.6	0.7	0.6
Tephrosia forbesii	0.8	0.4	0.8	-
Waltheria indica	2.5	7.5	7.0	0.1

which contained up to 7.5% polyphenol. All the other forbs contained from 0 - 2.5% polyphenol, considerably less than in any of the woody plant species. T. forbesii and S. panduraeforme contained less than 1% polyphenol at all times. The dried foliage of many forbs, including W. indica, contained virtually no polyphenols (Fig 5.26.)

ii. Alkaloids

Alkaloids were present in all but one species of forb tested (Table 5.38.). J. flava was rich in alkaloids and S. panduraeforme and T. forbesii also gave strong reactions with Mayer's and Dragendorff's reagents. Most forbs formed a [illegible]e precipitate with Mayer's reagent but for I. macra the [illegible] as weak. No alkaloids were detected in W. indica.

iii. Cyanogenic glycosides

Cyanogenic glycosides were only detected in small quantities in flowering and pre-flowering plants of J. flava.

iv. Saponins

Saponins were most common in mature forb plants. They were detected in the pre-flowering foliage of H. grisea, S. cordifolia and S. panduraeforme. (Table 5.39.). The mature plants of all forb species contained saponins, as detected by TLC but the post flowering plants of J. flava, P. campestris and S. panduraeforme

Table 5.38. The Presence of Alkaloids in Whole Forbs. Detected by the Formation of a Precipitate with Meyers Reagent

Species	Pre-Flowering Oct - Dec	Flowering Plants Jan - Mar	Post-Flowering Apr - Jun	Dried Plants Jul - Sept
Evolvulus alsinoides	++	++	++	-
Hermannia grisea	+	++	++	+
Indigofera macra	+	+	-	+
Justicia flava	+++	+++	+++	+++
Oldenlandia herbacea	-	-	++	-
Pollichia campestris	++	+	++	+++
Sida cordifolia	++	++	++	++
Solanum panduraeforme	++	+++	+++	+++
Tephrosia forbesii	++	+++	++	+++
Waltheria indica	Ø	Ø	Ø	Ø

Meyers reagent

+++ = strong precipitation

++ = precipitation

+ = slight precipitation

(+) = clouding

Ø = no reaction

Table 5.39. The Presence of Saponins in Whole Forbs, Detected by Thin Layer Chromatography

Species	Pre-Flowering Oct - Dec	Flowering Plants Jan - Mar	Post-Flowering Apr - Jun	Dried Plants Jul - Sept
Evolvulus alsinoides	Ø	+	+	-
Hermannia grisea	+	+	+	+
Indigofera macra	-	+	+	-
Justicia flava	Ø	+	Ø	+
Oldenlandia herbacea	-	+	+	+
Pollichia campestris	Ø	+	Ø	Ø
Sida cordifolia	+	+	+	Ø
Solanum panduraeforme	+	+	Ø	Ø
Tephrosia forbesii	Ø	+	+	+
Waltheria indica	Ø	+	+	+

TLC + = present

Ø = absent

contained no saponins. S. cordifolia was only free of saponins in the late dry season.

v. Mono- and Sesquiterpene Lactones

These lower terpenoids were detected in all the forbs at all growth stages. T. forbesii gave a particularly strong reaction with the test reagents but was not aromatic.

vi. Ether-extractable Compounds

Forbs contained between 1% and 5% ether-extractable materials. T. forbesii, H. grisea and the older foliage of S. panduraeforme were richest in ether-extract while least was found in E. alsinoides, J. flava and S. cordifolia (Table 5.40.). Concentrations of ether-extractable compounds showed little seasonal change appart from being very slightly higher in the post-flowering phases of the perennial species (Fig 5.27.).

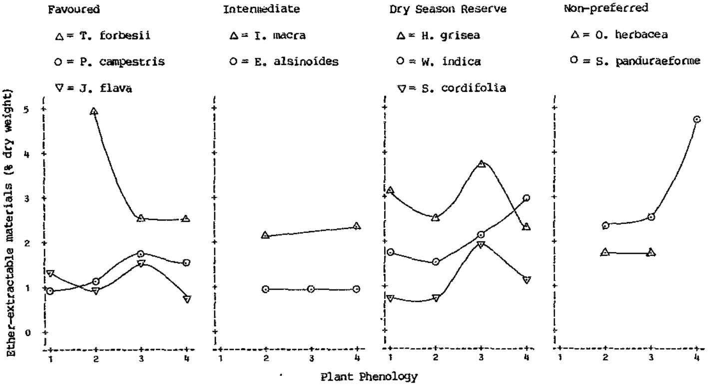


Fig 5.27. Changes in the concentration of Ether-extractable materials in whole forbs throughout the year. Plants grouped according to their acceptance to browsing ungulates.

Table 5.40. Concentrations of Ether-extractable Materials (% Dry Weight) in Composite Samples of Whole Forbs.

Species	Pre-Flowering Oct - Dec	Flowering Plants Jan - Mar	Post-Flowering Apr - Jun	Dried Plants Jul - Sept
Evolvulus alsinoides	-	1.0	1.1	1.1
Hermannia grisea	3.2	2.6	3.7	2.4
Indigofera macra	-	2.2	-	2.4
Justicia flava	1.4	0.9	1.6	0.8
Oldenlandia herbacea	-	1.8	1.8	-
Pollichia campestris	1.1	1.2	1.8	1.6
Sida cordifolia	0.7	0.8	2.1	1.2
Solanum panduraeforme	-	2.4	2.6	4.8
Tephrosia forbesii	-	5.0	2.5	2.5
Waltheria indica	1.8	1.5	2.3	3.1

Table 5.40. Concentrations of Ether-extractable Materials (% Dry Weight) in Composite Samples of Whole Forbs.

Species	Pre-Flowering Oct - Dec	Flowering Plants Jan - Mar	Post-Flowering Apr - Jun	Dried Plants Jul - Sept
Evolvulus alsinoides	-	1.0	1.1	1.1
Hermannia grisea	3.2	2.6	3.7	2.4
Indigofera macra	-	2.2	-	2.4
Justicia flava	1.4	0.9	1.6	0.8
Oldenlandia herbacea	-	1.8	1.8	-
Pollichia campestris	1.1	1.2	1.8	1.6
Sida cordifolia	0.7	0.8	2.1	1.2
Solanum panduraeforme	-	2.4	2.6	4.5
Tephrosia forbesii	-	5.0	2.5	2.5
Waltheria indica	1.8	1.5	2.3	3.1

5.4. DISCUSSION

1. Nutrients and Fibre

a. Nutrient Concentrations Recorded in Selected Browse Species

i. Species Occurring at Nylsvley

The nutrient contents of several of the more common browse plants in Africa have been analysed prior to this study. Comparison between studies is hindered by a lack of standardisation of techniques of analysis and failure to report exactly which plant parts have been analysed and what their phenological state was at that time.

However, the crude protein values of common browse plants at Nylsvley was generally similar to the values reported by Rushworth (1975), Bate (1979), Le Houerou (1980) and Novellie (1983,, but somewhat higher than those obtained by Dougall et. al. (1964) Bonsma (1976) and Jachman & Bell (unpublished).

Phosphorus contents were similar to those of Le Houerou (1980) and Novellie (1983), but higher than those of Dougall et. al. (1964) and Rushworth (1975).

Values for the potassium and magnesium contents of woody plants were similar in all the studies. The woody vegetion at Nylsvley appears to be lower in calcium and sodium than is reported for the same species growing in different areas. Only the values of calcium reported by Jachman & Bell (unpublished) were lower than those at Nylsvley.

ii. Genera Occurring at Nylsvley

The Acacia, Ziziphus and several Grewia species were particularly rich in protein and minerals. The Terminalia species were rich in calcium alone. Generally Terminalia and Diospyros species and evergreen genera Euclea and Ximenia were low in protein. Lannea, Combretum, Rhus and Vitex species were of intermediate nutrient levels, although the Lanneas were low in calcium (Dougall et. al. 1964).

Protein rich forbs species were of the genera, Achyranthes, Gomphrena, Ipomea, Hibiscus and Solanum species of Becium and Hermannia were low in protein and minerals. Mineral rich genera included Justicia, Gomphrena, Leucas, Hibiscus, Solanum, Indigofera and Tribulus. The latter two genera being especially rich in calcium. Tephrosia species were of low mineral content. Portulaca and Hermannia species were low in phosphorus and Labiate species and Asparagus were low in calcium (Dougall et. al. 1964).

b. Nutrients Contents in Ecosystems

i. Savannas

The nutrient content of browse plants varies considerably between plant species but on average the protein content of the vegetation at Nylsvley was similar to that found in other *Southern African* Savannas (Bonsma 1942, 1976, Groenewald et. al. 1967, Aucamp 1971, Roth & Osterberg 1971, Rees 1974, Rushworth 1975, Barnes 1976). The *protein content* of South African karroid shrubs is on average about 2-3% less than that of the savanna vegetation. East African savannas on soils of volcanic origin (Bell 1971) are more protein rich than Southern African savannas, particularly in the dry season when the crude protein level of many plants in East Africa remains above 15% (Dougall et. *al. 1964, Field & Ross* 1976, Le Houerou 1980). The crude protein concentration of browse plants in southern savannas is generally between 15% and 10% although newly emergent vegetation can contain as much as 30% protein for a brief period.

The phosphorus content of the vegetation at Nylsvley was in the region of 0.1 - 0.2%. This is less than that found in East Africa (*Field & Ross 1976*, Dougall et. al. 1964), but similar to the vegetation of Southern and West African savannas (Bonsma 1976, Le Houerou 1980).

Karoo shrubs (Louw et. al. 1973) and plants growing in Kalahari sand deposits in Zimbabwe (Rushworth 1975) *contain* approximately half the phosphorus content of other Southern African savanna plants.

The browse plants of Nylsvley were relatively poor in other minerals with calcium and potassium each constituting about 1% of the dry weight of the leaves, magnesium formed 0.25% of the leaf weight and sodium was present only in trace amounts. The Kalahari sands vegetation contained similar concentrations of these minerals to Nylsvley but all other savanna types contained almost double the concentrations of these minerals (Dougall et. al. 1964, Louw et. al. 1973, Bonsma 1976, Le Houerou 1980).

ii. Forests

The vegetation of the rainforest of Kibale in Uganda (Gartlan et.al. 1980, McKey et. al. 1978, Waterman et. al. 1980) was richer in crude protein than savanna vegetation. The soils of Kibale are fairly fertile sandy loams. Persistent plants of the Panama rainforest however showed similar nutrient levels to savanna vegetation (Coley 1983), or slightly less (Milton 1979).

The forests of Douala-Edea in the Cameroons (Gartlan et. al. 1980, McKey et. al. 1978, Waterman et. al. 1980), tropical Indian forest (Oates et. al. 1980) and Costa Rican forests (Glander 1981) are of rather lower protein and higher fibre content than the vegetation of Nylsvley and other savannas. Douala Edea forest is an evergreen tropical forest growing on highly acidic, hence nutrient poor soils derived from sandy marine sediments. In addition the rainfall is heavily seasonal (Gartlan et. al. 1980). The Indian forest is also a tropical evergreen forest growing under a heavily seasonal rainfall regime. The soils are stony (Oates et. al. 1980). The third, and most nutrient poor forest was the Costa Rican tropical dry forest (Glander 1981).

In all cases the nutrient content of the vegetation appeared to mirror the fertility of the soils.

iii. Montane Vegetation

The forest vegetation of Virunga mountains of Rwanda was rich in protein and nutrients and low in fibre (Waterman et. al. 1983) compared to South African savanna vegetation and to lowland forest vegetation of the same area (Waterman et. al. 1983). Most of the vegetation of the montane habitat consisted of non-woody plants.

iv. Temporate and Boreal Habitats

The vegetation of the USA (Radwan & Crouch 1971, Belovsky 1981, Vangilder et. al. 1982), and coniferous forests in Norway (Hjeljord et. al. 1982), was generally poor in crude protein and more fibrous than savanna vegetation. Mineral contents were however fairly high.

Tundra vegetation has an average crude protein concentration in mature leaves similar to that of savannas but is low in minerals (Chapin et. al. 1975, Batzli 1983). These plants require relatively high enzymatic levels in their tissues in order to function under very low temperature regimes (Chapin et. al. 1980b) so contain high nitrogen levels despite conditions of poor soil nutrient avilability.

b. Nutrient Contents of Grass, Forbs and Woody Plants

The range of nutrient contents in woody plants and forbs were very similar. The crude protein content of browse is generally considerably higher than that of grasses at all times except the early growing season. Grass supplies a surfeit of energy but is usually limiting in protein.

The protein level of tropical grasses frequently falls below 5% which is considered as the critical maintenance requirement of cattle (ARC 1965). Browse on the other hand rarely contains less than 8% crude protein in the late dry season and is often above 10% (Bonsma 1942, Dougall et. al. 1964, Groenwald 1967, Roth & Osterberg 1971, Rushworth 1975, Field & Ross 1976, Owen-Smith 1982). The vegetation of Nylsvley was no exception.

Grasses are generally lower in calcium than browse but slightly richer in phosphorus. Most plants contain adequate levels of potassium but very little sodium. The potassium content of forbs was generally slightly higher than that of woody plants. Leguminous species are frequently high in crude protein and low in fibre as compared to non-leguminous species (Dougall et. al. 1964).

c. Distribution of Nutrients between Plant Species

The nutrient concentration in browse plants varies greatly between species. The three deciduous thorny tree species analysed were noticeably rich in nutrients. All were of the leguminous subfamily Mimosoideae. Nitrogen fixation by root nodule bacteria is common in this subfamily (Grobelaar & Clark 1975), and leguminous plants are frequently high in protein (Dougall et. al. 1964). However the non-leguminous thorny tree Z. mucronata and the spiny forb S. panduraeforme were also comparatively rich in protein. Other nutrient rich species were the unarmed woody species G. flavescens and D. rotundifolia and the forb J. flava.

Evergreen plants are frequently very fibrous and consequentially low in nutrients. The evergreen shrub E. natalensis was indeed of low nutrient content. The other evergreen ...ies tested bore sharp terminal leaf spines and was richer in nutrients than E. natalensis.

The three ecological dominants of Burkea savanna, B. africana, T. sericea and O. pulchra were all of low nutrient status and withdrew nutrients from the leaves before leaf fall. B. africana is a leguminous species but does not harbour nitrogen-fixing bacteria (Grobelaar & Clark 1975), neither did the other common member of the Leguminous subfamily Caesalpinioideae P. africanum.

d. Seasonal Changes in Nutrient Concentrations in Browse Plants

Protein rich plants tend to be rich in other nutrients and conversely low in fibre. The concentrations of nitrogen, phosphorus and potassium were greatest in newly emergent foliage, declining sharply as the leaves achieved full size and began to harden. Thereafter a gradual build-up of cell wall components slowly diminished the relative amount of cell sap and presumably of soluble nutrients in the tissues. Crude protein contents of up to 25% dry weight were recorded for new leaves of Acacia trees and some forbs. Pellew (1982) found that the protein content of newly flushed Acacia shoots may reach 30% while the thorns are still soft.

Magnesium and sodium showed little seasonal change in concentration, but the results for sodium are suspect due to contamination caused by handling. In woody plants, but not forbs, calcium gradually accumulated. Much of the calcium in plant tissues is associated with the cell walls (Salisbury and Ross 1969).

Multivariate analysis of a wide range of plants by Garten (1978) distinguished three main sets of plant minerals. The first set, phosphorus, nitrogen, calcium, sulphur and iron were involved in the synthesis and maintenance of protein, amino-acids and nucleic acids. Magnesium, calcium and manganese formed a structural and photosynthetic group. Magnesium is central to chlorophyll and helps maintain ribosome structure, while calcium is found in plant cell walls. Magnesium and manganese were also correlated to potassium. These three minerals are important enzyme activators (Salisbury & Ross 1969).

Concentration of nitrogen and phosphorus were positively correlated in woody plants at Nylsvley but not in forbs where phosphorus seemed to be relatively independent of other minerals. Magnesium was most strongly correlated to calcium and potassium indicating that these minerals may fall *within* the structural and *enzymatic* sets of nutrients distinguished by Garten (1978). These relationships were most evident in the immature foliage of woody plants but the correlation broke down as the foliage matured.

e. Soil Nutrient Status and Nutrient Concentrations in the Vegetation

Plants obtain their nutrients from the soil. Hence the availability of soil nutrients is often reflected in the vegetation. Plants growing on impoverished soils tend to be of lower nutrient status than those growing on *richer soils* (Grimsdell & Bell 1974, *Gartlan et. al.* 1980).

The soils of the Acacia patches at Nylsvley are enriched with phosphorus compared to the surrounding soils supporting Burkea savanna (Harmse 1977). The woody plant species growing in these enriched sites were generally of higher nutrient content than the dominant species of the Burkea savanna. This *pattern* was also *reflected in the forb* component. However within the Burkea savanna a few species were of equally high nutrient status to those of the Acacia savanna. Microsite differences may explain the occurrence of nutrient rich species in the Burkea savanna. For example G. flavescens occurs on old ant hills which are probably of enhanced nutrient status.

2. Plant Secondary Compounds

a. Plant Secondary Compounds in Savannas and Other Ecosystems.

Virtually no quantitative informatiom is available on the secondary compounds present in savanna plants other than those substances of medical significance or injureous to livestock. A preliminary screening of some of the common woody plants at Nylsvley by Glennie (unpublished) merely confirms the findings of this study.

i. Toxins

Although cyanogenic activity is frequently repo ɔd for A. tortilis (Watt & Breyer-Brandwijk 1962) no trace of cyanogenic glycosides was detected in this species at Nylsvley. Polymorphism is commom in cyanogenic plants and has been proven in Acacia farenesiana (Seigler et. al. 1979, Janzen et. al. 1980), so probably occurs in other Acacia species. No cyanogenic activity has been reported for the other Acacia species occurring at Nylsvley and none was found in this study.

ii. Ether-extractable Compounds

Ether-extractable compounds generally constitute less than 5% of the dry mass of savanna plants and at the most 10% (Dougal et. al. 1964, Louw et. al. 1973, Rushworth 1975, Field & Ross 1976.)

Resins are far more abundant in cold-climate vegetation. In Alaska ether-extractable resins may account for 40% of the dry mass of overwintering twigs (Bryant 1981a).

iii. Phenolic compounds

The concentrations of total polyphenols and condensed tannins measured in A. tortilis at Nylsvley were similar to those found by Wrangham & Waterman (1981) for the same species in Amboseli, Kenya. Other than this study most of the work on polyphenol contents of natural vegetation refers to tropical forests.

i.) Total Polyphenols

The total polyphenol content of leaves of woody plants at Nylsvley ranged from 0 to 30% dry weight when measured by the Jerumanis method, or 0 to 17% with the commonly used Folin-Denis method. The range of total polyphenol contents in plants of many ecosystems was similar to that at Nylsvley. This includes tropical forests (McKey et. al. 1978, Milton 1979, Gartlan et. al. 1980, Oates et. al. 1980, Waterman et. al. 1980a), African montane vegetation (Waterman et. al. 1983) and strandveld (Puttick & Glyphis 1980).

Plants containing higher concentrations of total polyphenols occurred in the nutrient poor forests (Gartlan et. al. 1980, Coley 1983) and in Alaskan vegetation (Prudhomme 1983). Phenolic compounds are particularly prevalent in the genus Eucalyptus, the leaves of which may contain in excess of 40% polyphenols (Macauley

& Fox 1980). Eucalyptus species grow under conditions of low soil nutrient availability and are also rich in terpenes and low in nitrogen.

The lowest concentrations of polyphenols were found in African montane vegetation which is mainly herbaceous (Waterman et. al. 1983), and in the nutrient rich forests of Uganda (McKey et. al. 1978. Gartlan et. al. 1980, Waterman et. al. 1980a).

ii.) Condensed Tannins

The mature leaves of woody plants at Nylsvley contained between 0 and 13% condensed tannins relative to a Sorghum III tannin standard. Similar ranges of condensed tannin contents were recorded for African montane vegetation (Waterman et. al. 1983) and the nutrient rich forests of Uganda (McKey et. al 1978, Gartlan et. al. 1980, Waterman et. al. 1980a), but the averaged condensed tannin contents of the vegetation in these two ecosystems was less than for the Nylsvley plants. This indicates a greater occurrence of high tannin plants in the savanna.

In several plant species of the nutrient poor forests, and some Eucalyptus species, condensed tannins constituted a quarter of the dry weight of the leaves (McKey et. al 1978, Gartlan et. al. 1980, Oates et. al. 1980, Waterman et. al. 1980a, Macauley & Fox 1980, Coley 1983). The average contents of condensed tannin in these forests was much higher than that measured in savanna vegetation. As a note of caution it must be remembered that condensed tannins in the savannas were measured relative to a different standard to that used in the forest studies, Quebracho tannin being unavailable in South Africa.

b. Distribution of Plant Secondary Compounds in Grasses, Forbs and Woody Plants

Plant secondary compounds are characteristic of browse plants but are uncommon in grasses. At Nylsvley polyphenols were characteristic of the woody vegetation, while alkaloids were prevalent in the forb species. This is characteristic of most vegetation (Feeny 1976, Rhoades and Cates 1976). Substances with both digestion-reducing and toxic properties, such as saponins and terpenes were found in both woody plants and forbs.

c. Differences in the Commitment of Plant Species to Defensive Compounds

If chemical defence is costly to the plant in terms of resource allocation, it is to be expected that plants with structural or other defences will be low in chemical defences. Rehr et. al. (1972) showed that the foliage of South American Acacias, which are defended by mutualistic colonies of ants, have little or no cyanogenic activity, while the leaves of non-ant Acacias are bitter and cyanogenic.

The leaves of the deciduous thorny species at Nylsvley were however rich in polyphenols despite having sharp thorns. The one thorny evergreen plant contained little polyphenol but did contain alkaloids. Thorns are dead structures and once formed have little or no maintenance cost. They are effective against large herbivores but the plant must still be defended against insect herbivores and pathogens.

Evergreen plants are highly apparent to herbivores and hence require strong defences. In addition, evergreen plants tend to lack major storage reserves in the stems and roots for regrowth after defoliation (Bryant et. al. 1983). Such plants tend to be defended by digestion-reducing compounds, as was the case for the evergreen E. natalensis which was rich in condensed tannins. The other evergreen, S. pungens, however contained little polyphenols and no condensed tannins. In contrast to that predicted by the theory of apparency this plant was defended by alkaloids.

d. Seasonal Change in the Defensive Commitment of Plant Species

A plant's commitment to defence is related to the value of that tissue to the plant in terms of fitness lost should it be subject to herbivory (Feeny 1976, Rhoades and Cates 1976). Qualitative defences are usually highest in young tissues of apparent plants or in the case of forbs just prior to seed set (Jones 1950, McKey 1974).

The tests for alkaloids and cyanogenic glycosides used in this study were too simple to detect changes in tissue concentrations of these toxins, but two woody plant species showed the presence of alkaloids in their immature leaves alone. Similarly cyanogenic activity was detected only in the period before seed-set in J. flava.

Enzyme-inhibiting polyphenols, ether-extractable compounds and *saponins increased* in concentration as the vegetation matured, then decreased during senescence and presumably were degraded and re-utilised by the plants once the leaves became old and the fitness loss to herbivory decreased (McKey 1979, Zucker 1983, Drozdz 1962).

It has been suggested that immature leaves of woody plants do not contain carbon-based defences due to the problem of sequestering these substances away from the cell machinery (Orians and Janzen 1974, Feeny 1976, Rhoades and Cates 1976, McKey 1979). But evidence is accumulating that the young leaves of some plants may contain exceedingly high levels of phenolics (Rhoades and Cates 1976, Gartlan et. al. 1980, Coley 1983). This is in direct contrast to the prediction of the theory of apparency.

d. Environmental Conditions and the Cost of Defence

A major component of the apparency model is the relative cost of qualitative and quantitative defence. Qualitative defences were thought to be less costly to the plant in terms of resources diverted from growth because they are active in small quantities. However, qualitative defences such as *alkaloids have a rapid* turnover rate within the plant. These substances often contain nitrogen. The carbon-based *quantitative* defences in contrast have a slow rate of turnover. Hence over a period of time there may be little difference in the cost of the two different types of defence (Swain 1978, Fox 1981). In fact carbon-based defences may be cheaper than nitrogenous defences to plants growing under conditions of poor nutrient availability but with adequate light for photosynthesis.

An alternative to the *apparency model* is the theory that habitat quality may be a major selective force in determining the defensive strategy of the plants (Coley 1983, Bryant et. al. 1983).

In environments where rapid growth is possible plants are able to replace lost leaves at less cost than plants which live in low resource environments and have a slow growth rate and a low capacity for compensatory growth. The advantage of defence should increase as the potential maximum growth rate declines. Hence when the growth potential is high poorly defended species should be favoured, but when the potential for growth is low, relative to herbivory, the plants require strong constitutive defences.

Coley (1983) found that fast growing pioneer forest plants had a lower commitment to fibre and phenolic constituents than *persistent species* growing in the understorey where competition for nutrients is more severe. Similarly in a study of two African rain forests, one growing on acidic white sand soils and the other on fertile lateritic soils, Gartlan et. al. (1980) found the phenolic content of the vegetation growing under nutrient poor conditions to be double that of the vegetation growing on fertile soils. Alkaloidal species were more common in the nutrient rich forest.

Boreal vegetation grows under very different climatic conditions to tropical forest vegetation, yet again plants adapted to low resource environments have evolved strong carbon-based defences, this time phenolic resins rather than tannins, while the more rapid growing plants of higher quality environments are only heavily defended against browsers when in the juvenile phase and rapidly grow out of reach of browsers (Bryant et. al. 1983).

The savanna plants at Nylsvley grow on sandy soils of fairly low nutrient status, hence it is expected that the commitment to carbon-based defences will be high. In both the Burkea and Acacia savannas high levels of phenolic defences were found, particularly in the dominant plant species. The higher nutrient status of the soil in the Acacia patches was not reflected in a lower commitment of the plants to phenolic compounds.

The distribution of defensive compounds in the savanna vegetation at Nylsvley can be explained by either the apparency model (Feeny 1976, Rhoades and Cates 1976) or by habitat quality (Coley 1983, Bryant et. al. 1983). Both models have their advantages and disadvantages. The apparency model was initially based on erroneous calculations of the relative cost of qualitative and quantitative defences, yet the habitat quality model fails to explain why forbs should have predominantly nitrogen-based qualitative defences even when growing in nutrient poor habitats where the woody plants are heavily committed to carbon-based defences.

5.5. SUMMARY OF RESULTS

i. The savanna vegetation at Nylsvley was of similar nitrogen and phosphorus content as other Southern African savannas, but was low in other minerals. Values for specific plant species reflect the same pattern of nutrient concentration. Southern African savannas are less nutrient rich than those of equatorial Africa, particularly in the dry season.

ii. Savanna vegetation is more nutrient rich than evergreen tropical forests and coniferous forests where soil nutrient availability is low. Forests growing in nutrient rich soils and African montane vegetation contained higher levels of nitrogen and minerals than savannas.

iii. There is great seasonal and inter-species variation in the nutrient levels of browse plants. In the dry season the crude protein content of tropical grasses frequently falls below the critical maintenance requirement of ungulates, but browse plants usually contain around 10% protein even in the late dry season.

iv. The woody plant species at Nylsvley contained high levels of phenolic defences. Forbs contained mainly alkaloids. The presence of structural defences does not indicate a low commitment to chemical defences in the plants. Virtually no information is available on the concentrations of defensive compounds in the vegetation of other savannas.

v. African montane vegetation and tropical forests growing on fertile soils contained a smaller proportion of tannin rich species than occurred at Nylsvley. Very high concentrations of phenolic defences were found in the nutrient poor foliage of tropical evergreen forests and Eucalyptus trees.

vi. The quantitative defences of cold-climate plants tend to be phenolic resins rather than tannins. Resins are uncommon in savanna and tropical forest vegetation. However, concentrations of resins show the same relationship to habitat quality as do the tannins of plants from warmer climes.

FACTORS INFLUENCING THE UTILIZATION OF WOODY PLANTS AND FORBS BY UNGULATES

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(PART II : Chapters 6 to 11)

CHAPTER 6.

THE EFFECT OF PLANT STRUCTURE ON SPECIES SELECTION AND UTILISATION BY BROWSING UNGULATES

6.1. INTRODUCTION

Nutrient availabilities to the herbivore are influenced not only by the concentrations within plant tissues, but also by associated factors controlling the rates of ingestion. These include morphological features of the plants, such as the growth-form of the plant, the size of the leaves and their distribution on the less nutritious stems, and the presence of structural deterrents such as thorns and spines.

Several studies suggest that thorns are a defence against foliage loss to large herbivores (Brown 1960, Carlquist 1974), but there is little experimental evidence. However, phytophagous insects are not likely to be a causal agent in the evolution of large thorns and spines on plants. In Africa where browsing pressure by large herbivores is high, both at the present time and historically, the Acacias and many other plants are heavily thorned (Brown 1960). Armed plants are also common in tropical America. Although there are few native browsing animals in this area now, large browsers were abundant until fairly recently (Brown 1960, Janzen & Martin 1982) and thorniness is often retained as a juvenile trait (Kowlowsky 1971). In Australia no such radiation of large browsers seems to have taken place and few trees are thorny. Small browsers do occur and several of the low growing shrubby Acacias which are within the reach of these browsers do bear thorns, even some grasses are spiky (Brown 1960). The lack of armature is also characteristic of many oceanic islands, although some plants may be thorny in the juvenile phase (Carlquist 1974).

The distribution of spines on the plant suggests their defensive role against large herbivores. Many plants become less spiny as they grow out of reach of browsers. The lower branches branches of Acacias where the foliage is potentially within reach of browsers are often heavily armed. Similarly the leaves of Holly (Ilex aquifolium) on the lower branches are exceedingly spiny while crown leaves are smooth (Crawley 1983).

Many thorny species can facultatively increase their thorniness when browsed (Janzen 1981). The prickles on browsed plants of Rubus species are longer and sharper than those on nearby unbrowsed plants (Abrahamson 1975). Around a Sudanese settlement, Sey el Din and Obeid (1971) noticed that Acacia radiana, when browsed by goats, produced stunted branches covered in stiff thorns, while Acacia senegal, which does not have this ability, merely died out.

There is often an increase in the proportion of spinescent plants in heavily grazed areas suggesting avoidance by the animals (Papageorgiou 1979). The presence of Solanum species is often an indicator of overgrazing in Southern African Acacia veld (Grunow pers. comm.). Similarly Papageorgiou (1979) recorded that on a Greek island overgrazed by goats, the vegetation was characterised by a spiny shrub association, while the nearby goat-free islet was characterised by unarmed palatable plants.

Many thorny plants are however eaten by large herbivores suggesting that they may be of high nutritional value. The effects of plant structure on food selection by large herbivores will vary for animals with different feeding strategies.

6.2. METHODS

The influence of plant structure on the acceptance of common plant species to kudus, impalas and goats was considered in terms of:-

i. plant height,

ii. intake rate achieved,

iii. leaf size and the leaf to stem weight ratio of shoots,

iv. the presence of structural defenses.

The average weight of single leaves and the ratio of stem weight of shoots of a size eaten by the animals was calculated from composite samples of 100 leaves or a minimum of 10 shoots. Values are expressed in terms of dry weight. The intake rate was calculated as described in chapter 4.

The effect of structural defenses was examined in two experiments involving the removal of thorns from woody plants.

i. Removal of Thorns from Trees in the Veld

Ten trees each of Acacia burkei, A. nilotica, A. tortilis and Dichrostachys cinerea of a height accessible to impalas were selected in an area of the reserve adjacent to the enclosure for the tame animals. On each tree two branches were matched for size, shape, density of leaf cover and ease of access for browsers. The paired branches were labelled and the thorns removed from one of the pair, while the other was left intact. The relative loss of foliage due to browsing was estimated visually two months after the initiation of the experiment in December 1981.

ii. Removal of Thorns on Branches Presented to Penned Goats

Twelve branches of each of the armed species A. burkei, A. nilotica, A. tortilis, D. cinerea and Strychnos pungens, representing a variety of thorn and spine shapes and leaf sizes, were cut and matched for size, shape and density of leaf cover. For each species the thorns and spines of six branches were carefully removed. All the branches were labelled and weighed. One clipped and one unclipped branch were kept as controls. The other ten branches were individually presented to single penned goats, starting with a clipped branch then in random order. The goats were only allowed to eat approximately 20% of the leaves on each branch in order to minimise any effects of depletion of the leaves or satiation of the goat. The branches were subsequently weighed and the uneaten control branches used to correct for weight loss due to transpiration. The intake rate of the goats could then be calculated. Intake and bite rates achieved were statistically compared using students "t" test. This experiment was repeated six times over a period of two weeks.

No penning facilities without natural vegetation present were available for use with the impalas and kudus. This experiment was repeated with the impalas but they preferred to eat the grass in the pen rather than the hand-held branches. When the branches tied to the fence instead of being hand-held the impalas merely tossed them around with the horns and still did not eat any of the leaves.

6.3. RESULTS

1. Plant Characteristics

i. Plant Size

At Nylsvley the major cohort of woody plants with foliage within reach of the browsing ungulates consisted of shrubs and juvenile trees of under 0.5m high. These plants, which formed 40% of all woody plants, are within the herbaceous layer and hence are susceptible to both browsing and fire. The next most common cohort was shrubs of 0.5 - 1.5m in height and trees of above 2.5m. Most of the foliage of these trees is out of reach of the browsing ungulates. Few plants of the intermediate size occurred (Fig 6.1.).

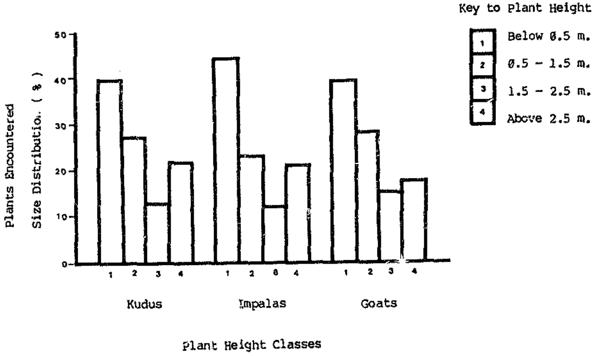

Fig 6.1. The Size Distribution of the Woody Plants Encountered by *Kudus, Impalas and Goats* (Excluding those plants on which no foliage was within the height reach of the animals)

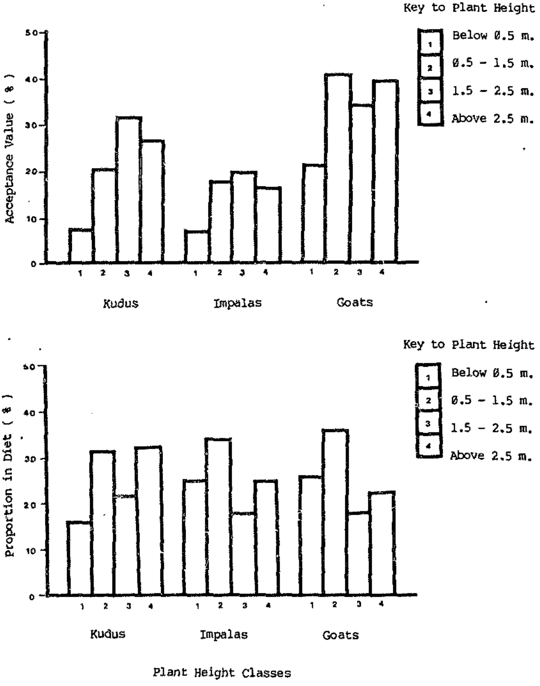

Fig 6.2. The Size Distribution of Woody Plants Relative to Acceptance and Utilisation by Browsing Ungulates.

All the animals had the lowest acceptance for the small woody plants growing within the herbaceous layer. The acceptances of plant within the other cohorts were fairly similar (Fig 6.2.). Due to the relative scarcity of plants in 1.5 - 2.5 m. height class, most of the diet of the animals consisted of shrubs of 0.5 - 1.5m and trees. The kudus ate less of the smallest size woody plants than did the impalas and goats. When feeding in the herbaceous layer kudus tended to eat forbs rather than small woody plants.

ii. Bite Size Achieved by the Animals.

When feeding on forbs and most structurally undefended woody plants, the bite size of the kudus was significantly greater than that of the impalas and goats by a magnitude of 2-3 times (Tables 6.1. & 6.2.). The kudus usually bit off large shoots, whereas the smaller animal species ate small shoots and single leaves (Fig 6.3.). The average bite size of the goats when feeding on woody plants was consistently slightly higher than that of the impalas, but the difference was not significant. When feeding on forbs the bite size of impalas and goats was very similar. The average bite size achieved by animals when feeding on forbs was almost half that achieved from structurally undefended woody plants.

The presence of thorns or spines on the branches of woody plants limited the animals to eating single leaves. All three animal species therefore achieved very similar bite sizes from the Acacia species and D. cinerea trees. Although the bite size

Table 6.1.a. The Average Bite Size Achieved by Browsing Ungulate when Feeding on Woody Plants

	Kudus			Impalas			Goats		
Species	Mean	SE	n	Mean	SE	n	Mean	SE	n
Acacia nilotica	0.03 ±	0.00	29	0.03 ±	0.00	320	0.03 ±	0.00	91
Acacia tortilis	-	-	-	0.02 ±	0.00	213	0.03 ±	0.00	37
Burkea africana	0.79 ±	0.08	75	0.08 ±	0.00	8	0.20 ±	0.01	207
Combretum molle	0.37 ±	0.04	93	0.19 ±	0.01	184	0.26 ±	0.02	131
Dichrostachys cinerea	0.10 ±	0.01	457	0.08 ±	0.00	938	0.10 ±	0.00	351
Dombeya rotundifolia	0.46 ±	0.03	41	-	-	-	0.25 ±	0.08	526
Euclea natalensis	0.48 ±	0.04	36	0.14 ±	0.01	138	0.21 ±	0.01	1931
Grewia flavescens	0.27 +	0.01	766	0.05 ±	0.04	1065	0.09 ±	0.00	1333
Ochna pulchra	0.17 ±	0.01	250	0.10 ±	0.02	95	0.15 ±	0.01	120
Peltophorum africanum	-	-	-	0.37 ±	0.01	54	0.72 ±	0.08	5
Rhus leptodictya	0.44 +	0.02	16	0.09 ±	0.01	25	0.17 ±	0.01	178
Strychnos pungens	0.37 ±	0.01	179	0.06 ±	0.01	118	0.08 ±	0.01	146
Terminalia sericea	0.46 ±	0.06	[illegible]	0.22 ±	0.03	80	0.20 ±	0.04	24
Vitex rehmannii	[illegible] +	0.03	[illegible]	0.14 ±	0.02	17	0.14 ±	0.01	220
Mean Thorny Plants	[illegible] +	0.04	[illegible]	0.04 ±	0.02	3	0.05 ±	0.03	3
Mean Non-thorny Plants Excluding P. africanum	0.45 ±	0.04	10	0.14 ±	0.03	10	0.18 ±	0.02	10

Table 6.1.b. A comparison of the Average Bite Size (gms) Achieved by Kudus, Impalas and Goats when Feeding on Woody plants

	Goats : Impalas		Kudus : Impalas		Kudus : Goats	
Spp	t	n	t	n	t	n
Acacia nilotica	0.000	411	0.000	349	0.000	120
Acacia tortilis	0.000	[illegible]	-	-	-	-
Burkea africana	5.583***	215	7.246***	83	5.393***	282
Combretum molle	1.565***	315	2.714**	277	1.457	224
Dichrostachys cinerea	1.155	[illegible]	1.414	1395	0.000	808
Dombeya rotundifolia	-	-	-	-	2.858**	567
Euclea natalensis	1.807	2069			3.227**	1967
Grewia flavescens	1.109	2398	12.712***	1831	13.000***	2099
Ochna pulchra	0.945	215	6.037***	345	4.690***	370
Peltophorum africanum	1.837	59	-	-	-	-
Rhus leptodictya	1.600	203	4.103***	41	3.641***	194
Strychnos pungens	0.667	264	11.667***	297	8.744***	325
Terminalia sericea	0.557	104	1.799	96	1.166	40
Vitex rehmannii	0.000	237	4.388***	174	9.120***	377
Mean All Thorny Plants	0.063	6	0.159	5	0.101	5
Mean All Non-thorny Plants	0.346	19	2.311	19	1.872	20

(Significance Levels : * P < 0.05; ** P < 0.01; *** P < 0.001)

Table 6.2.a. The Average Bite Size (gms) Achieved by Browsing Ungulate when Feeding on Forbs

	Kudus			Impalas			Goats		
Species	Mean	SE	n	Mean	SE	n	Mean	SE	n
Evolvulus alsinoides	-	-	-	0.05 ± 0.00		5	0.06 ± 0.00		25
Hermannia grisea	0.23 ± 0.01		61	0.09 ± 0.01		169	0.10 ± 0.00		306
Indigofera macra	-	-	-	-	-	-	-	-	-
Justicia flava	0.11 ± 0.00		126	0.08 ± 0.00		33	0.08 ± 0.00		8
Oldenlandia herbacea	-	-	-	-	-	-	-	-	-
Pollichia campestris	0.31 ± 0.02		130	0.10 ± 0.00		43	0.08 ± 0.00		99
Sida cordifolia	0.52 ± 0.07		27	0.06 ± 0.00		156	0.05 ± 0.00		73
Solanum pandureaforme	-	-	-	0.11 ± 0.00		73	-	-	-
Tephrosia forbesii	-	-	-	0.04 ± 0.01		18	-	-	-
Waltheria indica	0.24 ± 0.01		215	0.11 ± 0.00		303	0.14 ± 0.00		271
Mean All Species	0.28 ± 0.07		5	0.08 ± 0.01		8	0.09 ± 0.01		6
Mean Matched Species	0.28 ± 0.07		5	0.09 ± 0.01		5	0.09 ± 0.02		5

Table 6.2.b. A comparison of the Average Bite Size (gms) Achieved by Kudus, Impalas and Goats when Feeding on Forbs

	Goats : Impalas		Kudus : Impalas		Kudus : Goats	
Species	t	n	t	n	t	n
Evolvulus alsinoides	0.[illegible]7	30	-	-	-	-
Hermannia grisea	0.378	409	2.985**	230	2.837**	367
Indigofera macra	-	-	-	-	-	-
Justicia flava	0.000	41	2.121*	159	2.121*	134
Oldenlandia herbacea	-	-	-	-	-	-
Pollichia campestris	0.633	142	4.696***	173	5.750***	229
Side cordifolia	0.400	229	7.667***	183	[illegible]431***	100
Solanum pandureaforme	-	-	-	-	-	-
Tephrosia forbesii	-	-	-	-	-	-
Waltheria indica	1.732	682	4.333***	518	3.162**	486
Mean All Species	0.045	14	1.045	13	1.045	11

(Significance Levels : * P < 0.05; ** P < 0.01; *** P < 0.001)

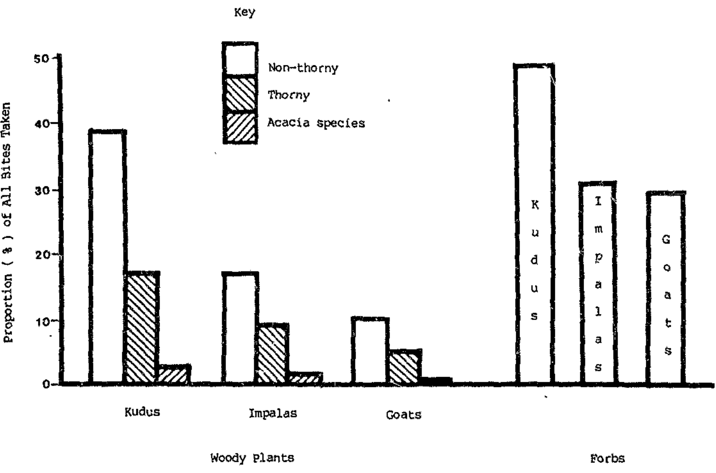

Fig 6.3. The Proportion of Shoot Bites taken by Kudus, Impalas and Goats

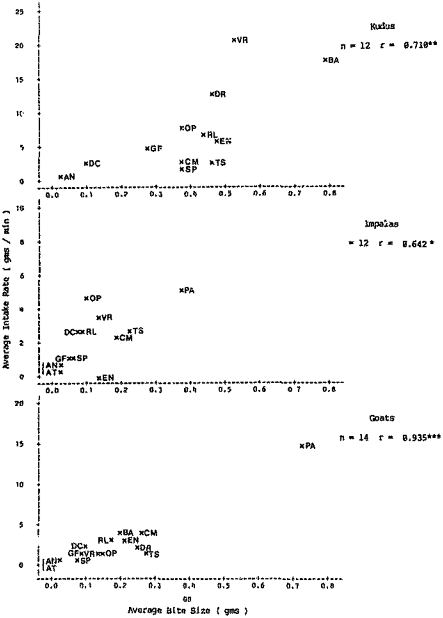

Fig 6.4. The Relation between the Bite Size Achieved by Browsing Ungulates and the Rate of Food Intake.

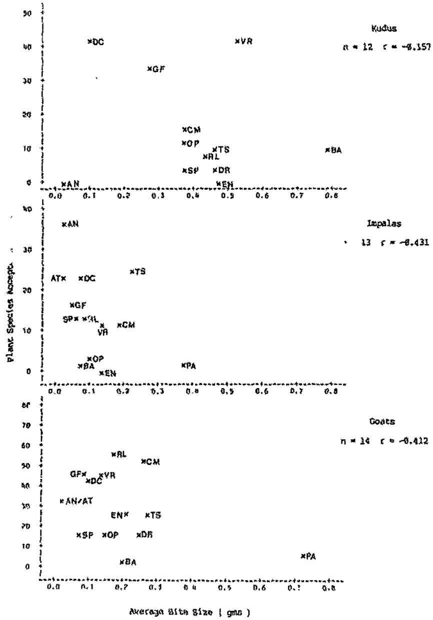

Fig 6.5. The Relation between the Acceptance of Woody Plant Species in the Late Growing Season and the Bite Size Achieved by Browsing Ungulates.

achieved by the animals was significantly correlated to the rate of food intake (Fig 6.4.), the acceptance of a plant species did not correlate with the size of bite obtained (Fig 6.5.).

iii. Biting Rate Achieved

The impalas generally had a significantly more rapid biting rate than the kudus and goats (Tables 6.3 & 6.4.). Unlike the bite size the biting rate was not related to the rate of food intake achieved (Figs 6.6. & 6.7.). The biting rate on woody plants was not significantly correlated to the acceptance of the woody plants (Fig 6.8.). Biting rates were most rapid when the animals were feeding on the thorny Acacia species which offer only a small bite size, and also on the favoured species D. cinerea, G. flavescens and V. rehmannii.

The impalas also had a rapid biting rate when feeding on S. pungens. They tend to pluck off single leaves in rapid succession rather than eating the shoots. The stems of S. pungens were very hard and every leaf bears a sharp terminal spine. The kudus had a low biting rate when feeding on these spiky shoots. Each shoot was bitten off with the molars then delicately turned around in the mouth until the spines pointed away from the throat before it could be swallowed. The goats ate mainly single leaves of this species but at a slower rate than the impalas.

The acceptance of forb species by impalas and goats was also

Table 6.3.a. The Average Biting Rate (bites / min) Achieved by Browsing Ungulate when Feeding on Woody Plants

	Kudus			Impalas			Goats		
Species	Mean	SE	n	Mean	SE	n	Mean	SE	n
Acacia nilotica	26.2 ±	5.5	4	27.4 ±	1.5	22	18.9 ±	2.2	10
Acacia tortilis	-	-	-	30.3 ±	2.1	15	38.1 ±	13.6	3
Burkea africana	16.6 ±	1.9	20	40.0 ±	-	1	19.3 ±	1.8	31
Combretum molle	13.3 ±	1.3	11	18.8 ±	1.7	20	13.9 ±	1.6	16
Dichrostachys cinerea	23.5 ±	1.1	61	20.1 ±	1.1	64	22.5 ±	1.6	36
Dombeya rotundifolia	15.6 ±	1.7	8	-	-	-	18.0 ±	1.0	68
Euclea natalensis	15.4 ±	4.2	7	23.5 ±	3.1	18	18.8 ±	1.0	206
Grewia flavescens	20.5 ±	1.0	90	34.4 ±	1.1	82	21.9 ±	0.8	112
Ochna pulchra	21.1 ±	1.5	34	26.2 ±	2.3	15	14.1 ±	2.3	16
Peltophorum africanum	-	-	-	18.9 ±	3.7	9	12.7 ±	0.7	2
Rhus leptodictya	17.0 ±	4.4	7	16.8 ±	2.3	6	14.6 ±	1.4	16
Strychnos pungens	12.4 ±	0.8	19	26.3 ±	1.9	27	16.3 ±	1.3	24
Terminalia sericea	13.1 ±	5.1	6	20.1 ±	3.4	14	14.7 ±	2.8	5
Vitex rehmannii	22.0 ±	1.5	16	28.7 ±	11.5	2	22.1 ±	2.1	18
Mean	18.8 ±	1.6	12	26.7 ±	2.3	13	19.0 ±	1.7	14

Table 6.3.b. A comparison of the Average Biting Rates Achieved by Kudus, Impalas and Goats when Feeding on Woody plants

	Goats : Impalas		Kudus : Impalas		Kudus : Goats	
Species	t	n	t	n	t	n
Acacia nilotica	7.441***	32	0.685	26	3.933**	14
Acacia tortilis	2.692*	18	-	-	-	-
Burkea africana	49.619***	33	40.165***	21	4.679***	51
Combretum molle	5.5[illegible]***	36	6.260***	31	0.674	27
Dichrostachys cinerea	0.800	100	8.693***	125	1.564	97
Dombeya rotundifolia	-	-	-	-	2.025**	76
Euclea natalensis	5.252***	224	5.319***	25	2.641**	215
Grewia flavescens	20.092***	194	12.383***	172	15.513***	202
Ochna pulchra	11.191***	31	5.529***	49	7.674***	50
Peltophorum africanum	5.474***	11	-	-	-	-
Rhus leptodictya	1.938*	22	0.124*	13	1.692	23
Strychnos pungens	12.639***	52	18.743***	46	5.853***	44
Terminalia sericea	3.672**	19	4.048***	20	0.876	11
Vitex rehmannii	2.275*	20	2.248*	18	0.071	34
Mean All Species	7.369***	27	7.532***	25	0.209	26

(Significance Levels : * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

Table 6.4.a. The Average Biting Rate (bites / min) Achieved by Browsing Ungulate when Feeding on Forbs

	Kudus			Impalas			Goats		
Species	Mean	SE	n	Mean	SE	n	Mean	SE	n
Evolvulus alsinoides	-	-	-	33.3 ±	-	1	15.4 ±	0.7	8
Hermannia grisea	23.9 ±	2.1	14	35.9 ±	3.3	19	34.3 ±	1.9	41
Indigofera macra	-	-	-	-	-	-	-	-	-
Justicia flava	33.9 ±	4.1	10	42.3 ±	7.3	2	28.2 ±	-	1
Oldenlandia herbacea	-	-	-	-	-	-	-	-	-
Pollichia campestris	35.1 ±	3.0	9	43.9 ±	7.0	5	35.5 ±	6.0	10
Sida cordifolia	19.7 ±	1.6	16	32.0 ±	2.0	17	35.1 ±	3.1	10
Solanum pandureaforme	-	-	-	30.8 ±	3.3	14	-	-	-
Tephrosia forbesii	-	-	-	42.9 +	10.3	4	-	-	-
Waltheria indica	27.4 ±	2.2	24	31.9 ±	1.9	44	27.7 ±	2.5	27
Mean	28.0 ±	2.9	5	36.6 ±	2.0	8	29.3 ±	3.1	6

Table 6.4.b. A comparison of the Average Biting Rates Achieved by Kudus, Impalas and Goats when Feeding on Forbs

	Goats : Impalas		Kudus : Impalas		Kudus : Goats	
Species	t	n	t	n	t	n
Evolvulus alsinoides	35.981***	9	-	-	-	-
Hermannia grisea	1.559	60	13.442***	33	17.915***	55
Indigofera macra	-	-	-	-	-	-
Justicia flava	6.249***	3	3.324**	12	5.089***	11
Oldenlandia herbacea	-	-	-	-	-	-
Pollichia campestris	3.035**	15	4.196**	14	0.011	19
Sida cordifolia	2.407*	27	11.841***	33	13.289***	26
Solanum pandureaforme	-	-	-	-	-	-
Tephrosia forbesii	-	-	-	-	-	-
Waltheria indica	4.415***	65	5.249***	68	0.290	45
Mean All Species	6.274***	14	7.308***	13	0.812	13

(Significance Levels : * P < 0.05; ** P < 0.01; *** P < 0.001)

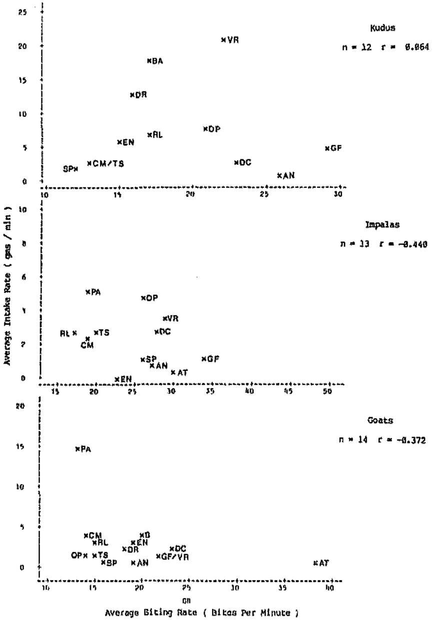

Fig 6.6. The Relation between the Biting Rate Achieved by Browsing Ungulates and the Rate of Intake of Woody Plants.

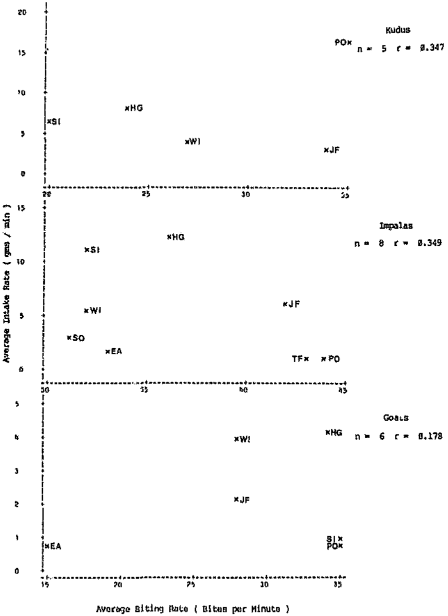

Fig 6.7. The Relation between the Biting Rate Achieved by Browsing Ungulates and the Rate of Intake of Forbs.

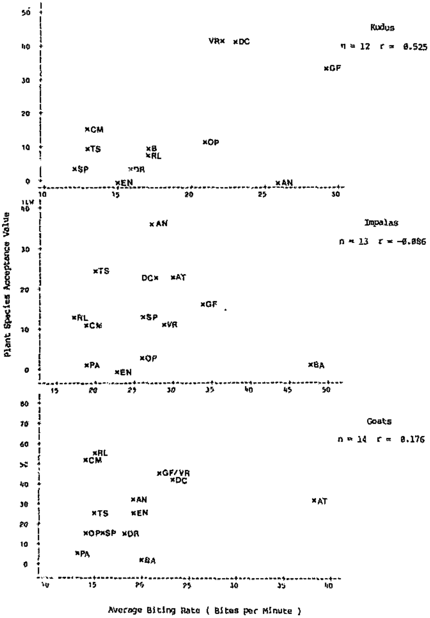

Fig 6.8. The Relation between the Acceptance of Forb Species in the Late Growing Season and the Biting Rate Achieved by Browsing Ungulates

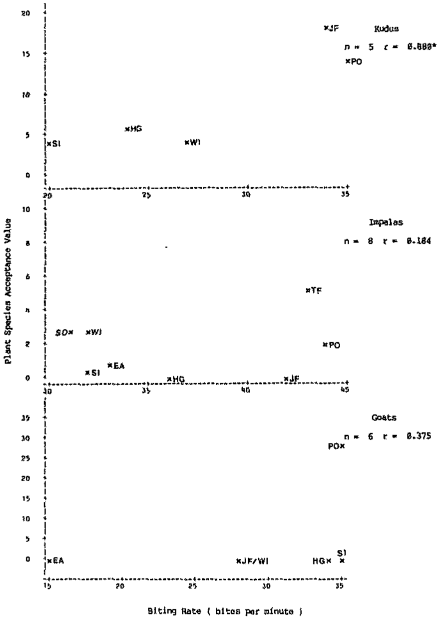

Fig 6.9. The Relation between the Acceptance of Woody Plant Species in the Late Growing Season and the Biting Rate achieved by Browsing Ungulates.

not correlated to the biting rate, but a significant correlation existed for the kudus due to their rapid rate of biting on the two favoured species P. campestris and J. flava (Fig 6.9.).

The rate of biting when feeding on forbs was generally more rapid than when eating woody plants. The forbs from which the highest biting rates were achieved were P. campestris and J. flava which do not have a very thick central stem. The impalas and goats both had a higher biting rate than the kudus when feeding on S. cordifolia and H. grisea. These two forbs are perennial species with hard stems. The kudus ate shoots while the impalas and goats nibbled the leaves off the side of the stems.

For woody plants the bite size and rate of biting (Fig 6.10.). were negatively correlated only when the two large leaved, non-favoured species B. africana and P. africanum were excluded (kudus $r = -0.617^*$, impalas $r = -0.636^*$, goats $r = -0.615^*$). The biting rate and bite size achieved from forbs were not correlated.

iv. Intake Rates Achieved

a. Woody Plants

The acceptance of plant species by kudus, impalas and goats was not significantly correlated to the intake rate achieved (Fig 6.11.). Many of the large leaved plants such as B. africana, P. africanum and the Lannea species offered a high rate of food intake but were of low acceptance (Table 6.5.a.). The acceptance

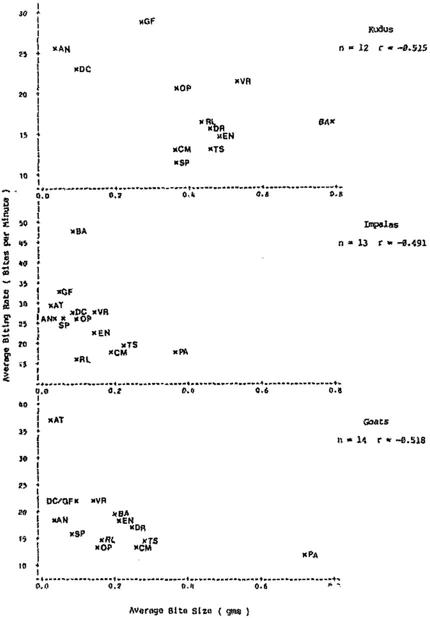

Fig 6.10. The Relation between the Bite Size and Biting Rate Achieved by Browsing Ungulates when Feeding on Woody Plants

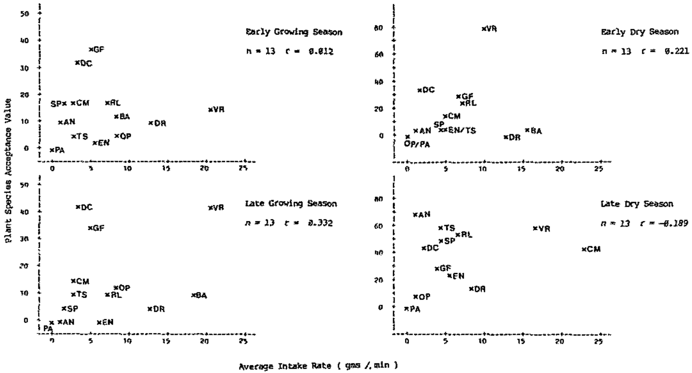

Fig 6.11. The Relation between the Acceptance of Woody Plant Species and Rate of Food Intake Achieved by Browsing Ungulates.

i. Kudus

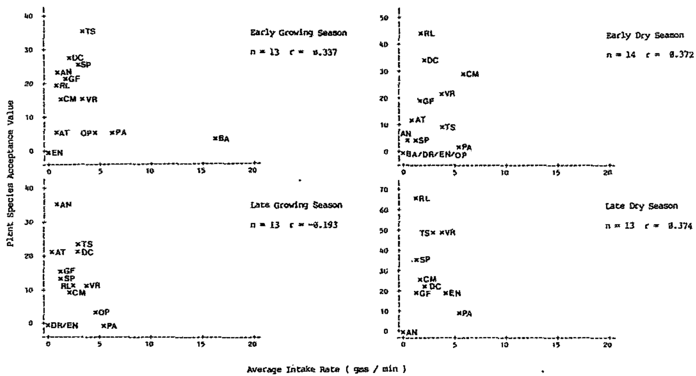

Fig 6.11. The Relation between the Acceptance of Woody Plant Species and Rate of Food Intake Achieved by Browsing Ungulates.

ii. Impalas

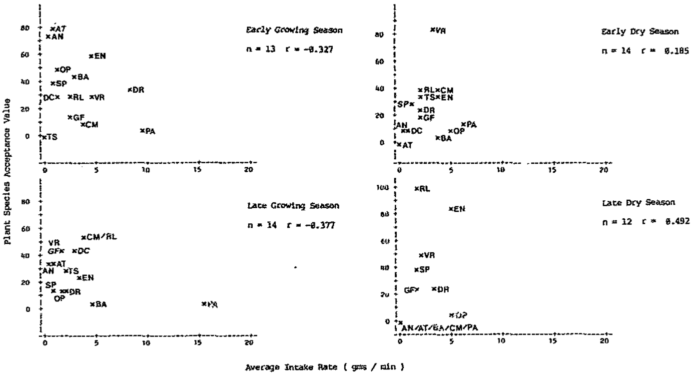

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Fig 6.11. The Relation between the Acceptance of Woody Plant Species and Rate of Food Intake Achieved by Browsing Ungulates.

iii. Goats

Table 6.5.a. The Average Intake Rate (gms / min) Achieved by Browsing Ungulate when Feeding on Woody Plants

	Kudus			Impalas			Goats		
Species	Mean	SE	n	Mean	SE	n	Mean	SE	n
Acacia nilotica	0.86	± 0.22	4	3.81	± 0.07	22	0.45	± 0.07	10
Acacia tortilis	-	-	-	0.66	± 0.07	15	0.76	± 0.27	3
Burkea africana	13.24	± 2.34	20	1.84	± -	1	3.75	± 0.45	31
Combretum molle	4.06	± 1.85	11	1.63	± 0.60	20	3.79	± 0.57	16
Dichrostachys cinerea	2.03	± 3.11	61	2.20	± 0.11	64	2.11	± 0.20	36
Dombeya rotundifolia	8.58	± 2.35	9	-	-	-	4.43	± 0.45	60
Euclea natalensis	6.09	± 0.99	7	1.38	± 0.58	10	4.17	± 0.26	206
Grewia flavescens	4.99	± 0.30	90	1.51	± 0.09	82	1.99	± 0.19	112
Ochna pulchra	5.78	± 0.71	34	2.58	± 1.03	15	2.33	± 0.53	16
Peltophorum africanum	-	-	-	6.42	± 0.87	9	9.71	± 0.71	2
Rhus leptodictya	7.25	± 0.98	7	1.45	± 0.31	6	2.62	± 0.56	16
Strychnos pungens	4.49	± 0.42	19	1.47	± 0.23	27	1.10	± 0.13	24
Terminalia sericea	4.66	± 0.93	6	3.10	± 0.55	14	4.08	± 0.46	5
Vitex rehmannii	11.01	± 2.65	16	3.59	± 0.27	2	3.15	± 0.74	18
Mean	6.23	± 1.04	12	2.67	± 0.44	13	3.17	± 0.61	14

Table 6.5.b. A comparison of the Average Intake Rates (gms / min) Achieved by Kudus, Impalas and Goats when Feeding on Woody plants

	Goats : Impalas		Kudus : Impalas		Kudus : Goats	
Species	t	n	t	n	t	n
Acacia nilotica	1.872	32	0.141	26	0.853	14
Acacia tortilis	0.240	18	-	-	-	-
Burkea africana	0.316	31	12.990 *	21	12.211***	51
Combretum molle	0.314	36	0.051	31	1.397	27
Dichrostachys cinerea	0.784	100	1.494	125	0.3659	97
Dombeya rotundifolia	-	-	-	-	4.409***	76
Euclea natalensis	2.054*	224	3.777***	25	3.094**	215
Grewia flavescens	2.869**	194	16.981***	172	13.416***	202
Ochna pulchra	0.394***	31	5.112***	49	6.832***	50
Peltophorum africanum	3.728**	11	-		-	-
Rhus leptodictya	2.264*	22			6.483***	23
Strychnos pungens	1.399	52	0.0[illegible]		9.705***	44
Terminalia sericea	1.649	19	2.149*	-	0.758	11
Vitex rehmannii	0.454	20	6.881***	18	9.466***	34
Mean All Species	1.209	27	9.526***	25	6.994	26

(Significance Levels : * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$)

Table 6.5 c Comparison of the Intake Rates Achieved by Browsing Ungulates when Feeding on Armed and Unarmed Woody Plant Species of Similar Leaf Size.

Description	Species Compared	Kudus		Impalas		Goats	
		t	n	t	n	t	n
Similar leaf Size, Armed	Acacia nilotica : Acacia tortilis	-	-	0.026	37	0.0711	13
Different Leaf Size, Armed	Acacia nilotica : Dichrostachys cinerea	3.105**	94	8.632***	86	7.078***	46
Similar Leaf Size, Armed and Unarmed	Acacia nilotica : Grewia flavescens	11.728***	65	4.430***	104	9.950***	122
Armed larger Leaved than Unarmed	Dichrostachys cinerea : Grewia flavescens	13.801***	151	4.970***	146	0.531	148
Leaves same Size, Spined versus Simple	Strychnos pungens : Grewia flavescens	1.398	99	1.721	109	4.565***	146

(Significance Levels : * P < 0.05; ** P < 0.01; *** P < 0.001)

of thorny species were of lower acceptance than other chemically similar species.

The kudus generally obtained a significantly higher rate of food intake than the impalas and goats when feeding on unarmed plants, but when feeding on thorny plants their intake rate was no different to that of the smaller animal species (Table 6.5.b.).

All the animals had a significantly lower rate of food intake when feeding on the thorny Acacia species than when feeding on a palatable, unarmed, species such as G. flavescens, which had a similar leaf size (Table 6.5.c.). The rate of food intake from D. cinerea was significantly higher than that obtained from the Acacia species, despite being similarly armed with stem spines. The leaves of D. cinerea are considerably larger than those of the Acacias (Table [illegible].5.), yet despite the larger leaf size, the rate of food intake achieved by the kudus when feeding on D. cinerea was still lower than that achieved from unarmed species even those with a smaller leaf size. This is because kudus mainly select shoots when feeding on unarmed species, whereas the bite size from thorny plants is limited to single leaves. Impalas often eat single leaves when feeding on unarmed plants and hence the intake rate achieved from D. cinerea was comparable with that of several unarmed species.

The intake rate of kudus when feeding on S. pungens, which offers a large bite size but a slow biting rate due to the spiny leaves, was comparable to that achieved from unarmed species with

Table 6.6. The Average Weight (gms Dry Weight) of Individual Leaves of Woody Plant Species

Species	Mean	Range
Burkea africana	1.63	0.72 - 1.88
Lannea edulis	1.04	0.34 - 1.08
Lannea discolor	0.99	0.31 - 1.33
Sclerocarya caffra	0.77	0.63 - 0.90
Vangueria infaustra	0.65	0.47 - 0.77
Peltophorum africanum	0.58	0.20 - 1.15
Bequartiodendron magalismontanum	0.50	0.42 - 0.59
Acacia caffra	0.24	0.23 - 0.33
Combretum zeyheri	0.22	0.14 - 0.54
Bridelia mollis	0.21	0.20 - 0.21
Grewia monticola	0.18	0.15 - 0.22
Combretum molle	0.10	0.07 - 0.51
Euclea natalensis	0.10	0.12 - 0.25
Mundulea sericea	0.17	0 .4 - 0.19
Vitex rehmannii	0.14	0.08 - 0.10
Ochna pulchra	0.14	0.07 - 0.47
Ozoroa paniculosa	0.14	0.08 - 0.20
Strychnos cocculoides	0.12	0.10 - 0.14
Dichrostachys cinerea	0.12	0.04 - 0.25
Dombeya rotundifolia	0.17	0.07 - 0.15
Terminalia sericea	0.10	0.06 - 0.19
Acacia heteroclada	0.10	0.10
Rhus pyroides	0.10	0.09 - 0.15
Rhus leptodictya	0.10	0.05 -0.15

Table 6.6. Continued...

Strychnos madagascariensis	0.09	0.08 - 0.09
Combretum apiculatum	0.08	0.07 - 0.23
Euclea crispa	0.08	0.08
Pseudolachnostylis maprounifolia	0.07	0.07
Ziziphus mucronata	0.07	0.03 - 0.13
Ximenia caffra	0.07	0.06 - 0.08
Cassine transvaalensis	0.06	0.05 - 0.06
Acacia karoo	0.06	0.04 -0.17
Grewia bicolor	0.05	0.05 - 0.06
Acacia burkei	0.05	0.04 - 0.09
Strychnos pungens	0.05	0.03 - 0.08
Grewia flavescens	0.04	0.02 - 0.06
Acacia nilotica	0.04	0.02 - 0.07
Grewia flava	0.03	0.02 - 0.06
Carissa bispinosa	0.03	0.01 - 0.06
Maytenus tenuispina	0.02	0.01 - 0.03
Ehretia rigida	0.02	0.01 - 0.04
Canthium gilfillanii	0.02	0.01 - 0.04
Acacia tortilis	0.02	0.01 - 0.03
Euclea undulata	0.02	0.02 - 0.04
Erythrococca menyharthii	0.01	0.01 - 0.02
Securidaca longipedunculata	0.01	0.01

a similar leaf size. The intake rate of the impalas on these species was also not significantly affected by the presence of leaf spines but these spines did lower the rate of food intake by the goats which tended to eat only single leaves and small shoots of 2-3 leaves.

b. Forbs

The rate of food intake achieved when feeding on forbs was not correlated to acceptance for any of the animal species (Fig 6.12.). Favoured species like J. flava and T. forbesii offerred only a low rate of food intake as compared to the less favoured stemmy perennial species. The kudus obtained a significantly higher rate of food intake from forbs than did the goats and impalas due to their larger bite size (Table 6.7.). The impalas had a higher rate of food intake than the goats when feeding on S. cordifolia and W. indica, due mainly to their more rapid biting rate.

v. Leaf Size and Leaf to Stem Ratio of Shoots

The size of the leaves of woody plants bore no correlation to the leaf to stem weight value of the shoots, except that species with very small leaves such as Securidaca longipedunculata naturally tended to have a low leaf to stem ratio (Fig 6.13.). Many of the thorny species such as Acacia species, Z. mucronata and C. bispinosa also had small leaves. Species with a high leaf to stem ratio were the Combretum species and plants such as T. sericea and

Table 6.7.a. The Average Intake Rate (gms / min) Achieved by Browsing Ungulate when Feeding on Forbs

	Kudus			Impalas			Goats		
Species	Mean	SE	n	Mean	SE	n	Mean	SE	n
Evolvulus alsinoides	-	-	-	1.67 ±	-	1	0.84 ±	0.18	8
Hermannia grisea	6.49 ±	1.05	14	4.53 ±	0.64	19	4.71 ±	0.39	41
Indigofera macra	-	-	-	-	-	-	-	-	-
Justicia flava	3.71 ±	0.44	10	3.30 ±	0.79	2	2.26 ±	-	1
Oldenlandia herbacea	-	-	-	-	-	-	-	-	-
Pollichia campestris	10.88 ±	3.60	9	3.32 ±	1.52	5	2.40 ±	1.00	10
Sida cordifolia	9.80 ±	2.21	16	2.79 ±	1.60	17	1.02 ±	0.25	10
Solanum pandureaforme	-	-	-	3.66 ±	0.37	14	-	-	-
Tephrosia forbesii	-	-	-	1.19 ±	0.21	4	-	-	-
Waltheria indica	6.38 ±	0.80	24	4.60 ±	0.59	44	2.99 ±	0.36	27
Mean	7.45 ±	1.29	5	3.14 ±	0.43	8	2.37 ±	0.58	6

Table 6.7.b. A comparison of the Average Intake Rate (gms / min) Achieved by Kudus, Impalas and Goats when Feeding on Forbs

	Goats : Impalas		Kudus : Impalas		Kudus : Goats	
Species	t	n	t	n	t	n
Evolvulus alsinoides	1.956	9	-	-	-	-
Hermannia grisea	2.937**	60	2.996**	33	3.044**	55
Indigofera macra	-	-	-	-	-	-
Justicia flava	1.498	3	0.436	12	1.916	11
Oldenlandia herbacea	-	-	-	-	-	-
Pollichia campestris	1.090	15	5.514***	14	7.640***	19
Sida cordifolia	2.527*	27	7.226***	33	11.722***	26
Solanum pandureaforme	-	-	-	-	-	-
Tephrosia forbesii	-	-	-	-	-	-
Waltheria indica	4.050	73	3.546***	68	7.038***	52
Mean All Species	1.127	14	0.679***	13	0.480***	11

(Significance Levels : * P < 0.05; ** P < 0.01; *** P < 0.001)

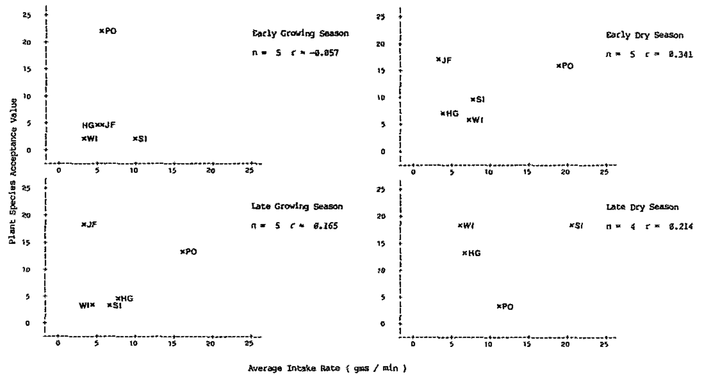

Fig 6.12. The Relation between the Acceptance of Forb Species and Rate of Food Intake Achieved by Browsing Ungulates.

i. Kudus

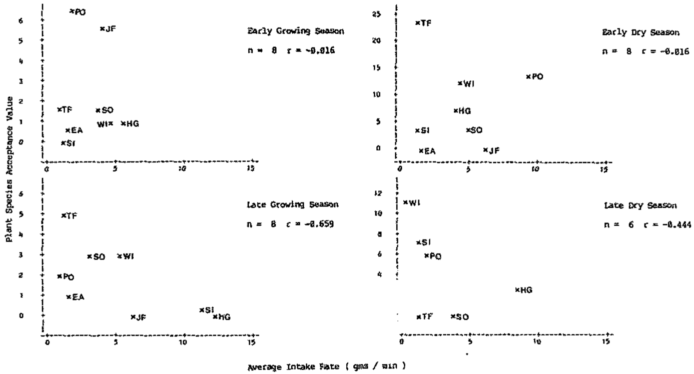

Fig 6.12. The Relation between the Acceptance of Forb Species and Rate of Food Intake Achieved by Browsing Ungulates.

ii. Impalas

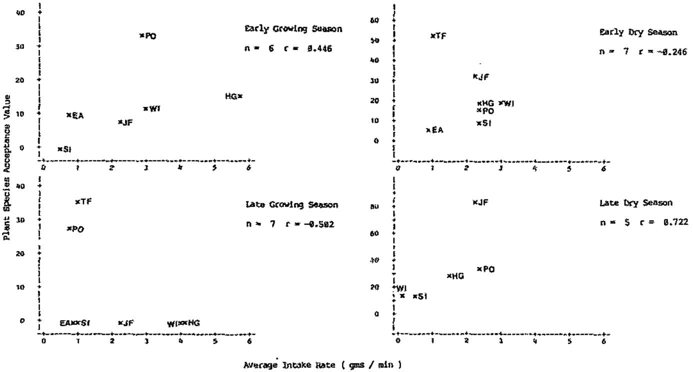

Fig 6.12. The Relation between the Acceptance of Forb Species and Rate of Food Intake Achieved by Browsing Ungulates.

iii. Goats

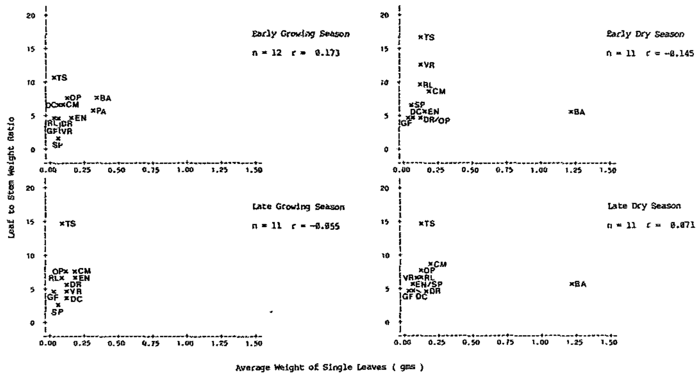

Fig 6.13. The Relation between the Size of the Leaves and the Ratio of Leaf to Stem Tissue in the Shoots of Woody Plants.

O. pulchra where the leaves grow in clusters.

The acceptance of woody species was not correlated to the leaf weight (Fig 6.14.), except in the early growing season, when the impalas displayed a significant preference for the small leaved plants. Noticeably all the animals had a very low acceptance for the two large leaved species B. africana and P. africanum.

The ratio of leaf tissue to fibrous stem of the shoots was also not correlated to the acceptance of plant species (Fig 6.15.). For the kudus in particular the large clusters of T. sericea leaves were of low acceptance.

The intake rate of the impalas was positively correlated to leaf size in the growing season (Fig 6.16.). Since impalas eat mainly single leaves this relationship was only to be expected. This correlation was evident, but less strong, for the goats and kudus in the growing season and did not reach significance. The intake rate of the kudus was correlated with leaf size in the dry season mainly due to the few occasions on which they ate the large leaves of B. africana, but for the goats and impalas the rejection of this species spoilt the correlation.

The relationship between the leaf to stem ratio of the plants and the intake rate was not significant for any of the animals. Many of the plants species with large leaves or leaf clusters enabling the browser to achieve a high potential bite size and

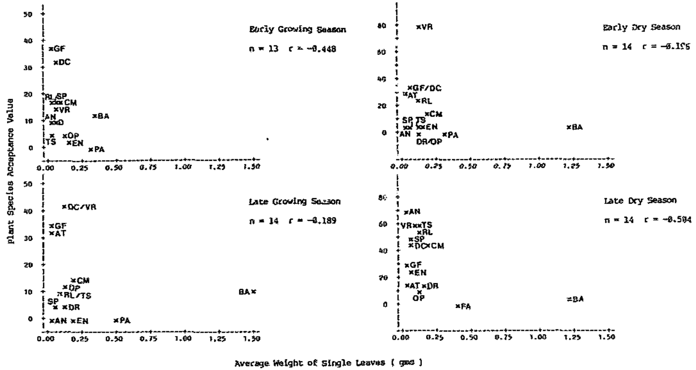

Fig 6.14. The Relation between the Acceptance of Woody Plant Species and the Average Weight of Individual Leaves.

i. Kudus

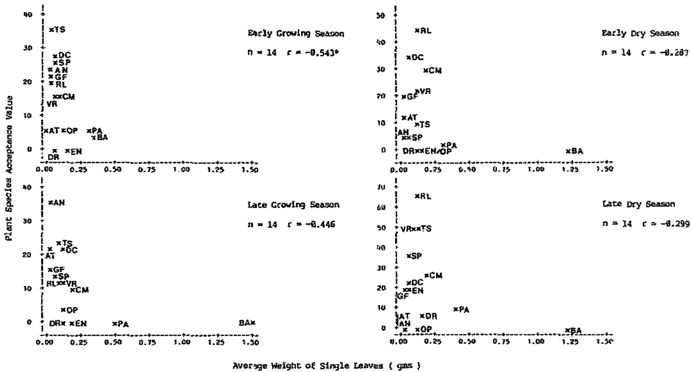

Fig 6.14. The Relation between the Acceptance of Woody Plant Species and the Average Weight of Individual Leaves.

ii. Impalas

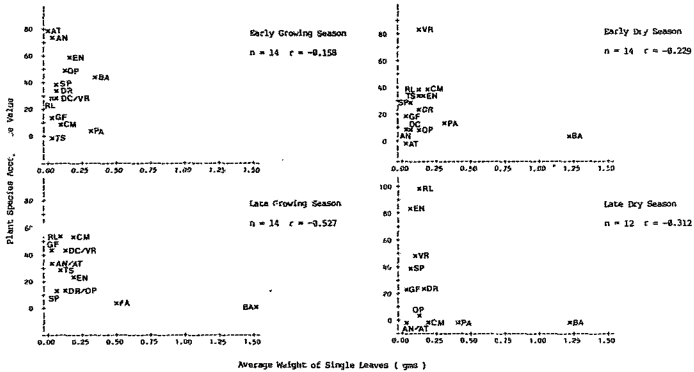

Fig 6.14. The Relation between the Acceptance of Woody Plant Species and the Average Weight of Individual Leaves.

iii. Goats

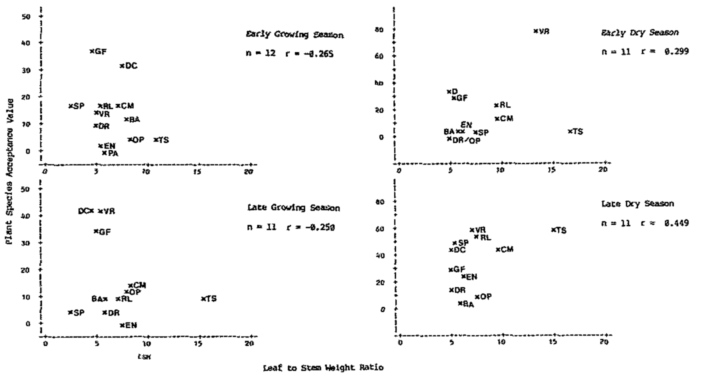

Fig 6.15. The Relation between Acceptance and the Ratio of Leaf to Stem Tissue in the Shoots of Woody Plants.

i. Kudus

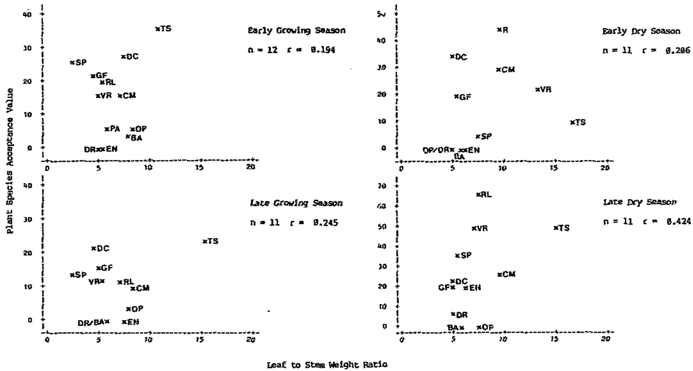

Fig 6.15. The Relation between Acceptance and the Ratio of Leaf to Stem Tissue in the Shoots of Woody Plants.

ii. Impalas

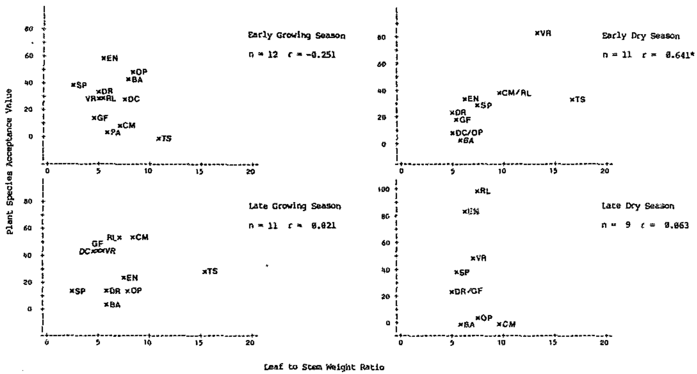

Fig 6.15. The Relation between Acceptance and the Ratio of Leaf to Stem Tissue in the Shoots of Woody Plants.

iii. Goats

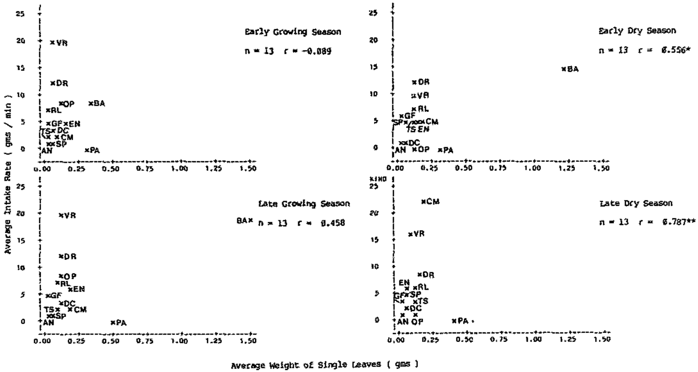

Fig 6.16. The Relation between the Rate of Food Intake Achieved and the Average Weight of Individual Leaves of Woody Plant Species.

i. Kudus

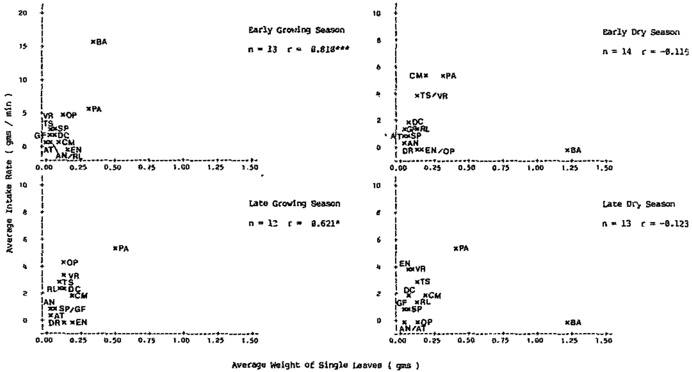

Fig 6.16. The Relation between the Rate of Food Intake Achieved and the Average Weight of Individual Leaves of Woody Plant Species.

ii. Impalas

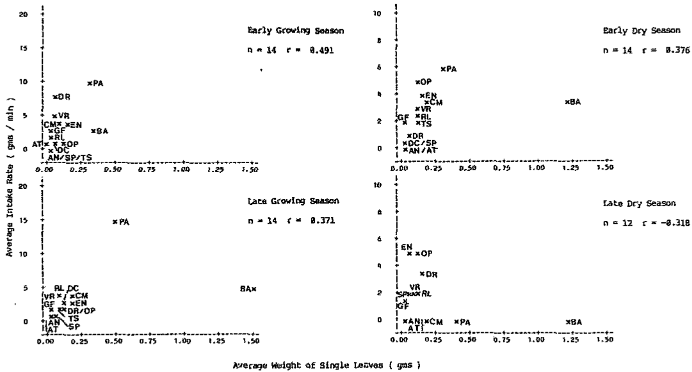

Fig 6.16. The Relation between the Rate of Food Intake Achieved and the Average Weight of Individual Leaves of Woody Plant Species.

iii. Goats

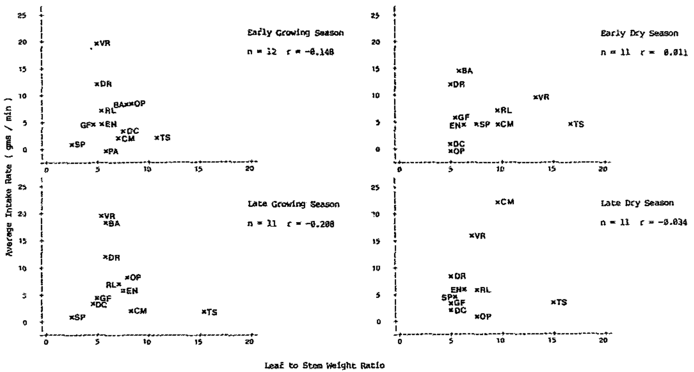

Fig 6.17. The Relation between the Rate of Food Intake Achieved and the Ratio of Leaf to Stem Tissue in the Shoots of Woody Plants.

i. Kudus

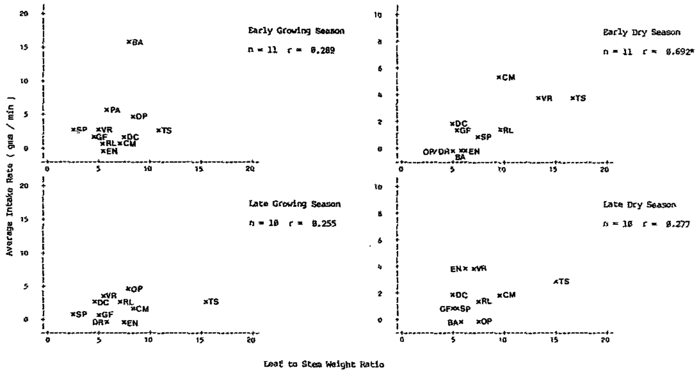

Fig 6.17. The Relation between the Rate of Food Intake Achieved and the Ratio of Leaf to Stem Tissue in the Shoots of Woody Plants.

ii. Impalas

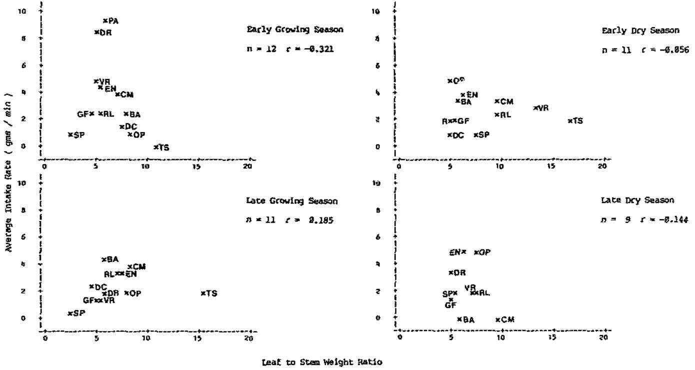

Fig 6.17. The Relation between the Rate of Food Intake Achieved and the Ratio of Leaf to Stem Tissue in the Shoots of Woody Plants.

iii. Goats

hence intake rate were infact of low acceptance to the animals. Conversely many favoured species had small leaves or were armed with thorns or spines. The acceptance of several large leaved species tended to increase in the dry season when food availability was low. There was no decrease in the acceptance of smaller leaved species except for the microphyllous Acacias species and D. cinerea. When dry these leaves disintegrated up on contact and hence the animals got very little to eat from these leaves.

2. Description of the Effect of Structural Deterrents on the Animals Method of Feeding

a. Woody Plants

When feeding on Acacia species all the animals were restricted to eating single leaves or small clusters of leaves growing between the thorns. A. tortilis, which has tiny leaves set in between both hooked and straight thorns, was rarely eaten by the kudus despite the high nutrient content of the foliage. The impalas also tended to have a lower acceptance for A. tortilis than A. nilotica which has larger leaves, although the foliage is slightly less rich in nutrients and contains more enzyme-inhibiting polyphenols than that of A. tortilis.

The hooked thorns of A. tortilis and A. burkei tended to catch on the lips and tongue of the feeding animal. The goats encountered additional problems when feeding on small A. burkei plants as their long floppy ears became painfully entangled in the large hooked thorns and it often took a considerable time for the goats to free themselves. The branches of Acacias also tend to be flexible. Often when an animal pulled off a leaf the branch swayed pricking the face of the feeding animal and preventing it from resuming feeding until the branch was steady once more.

The spines of D. cinerea were less sharp and more widely spaced than the thorns on Acacia plants, but still effectively limited the animals to eating single leaves. Similarly the spines of Maytenus tenuispina limited the bite-size to one leaf cluster.

The evergreen C. bispinosa had bifurcated spines and a dense growth form which limited access by large browsers. This plant was browsed by impalas and goats in the late dry season but was not often eaten by the kudus. The protein rich leaves of Z. mucronata were protected by hooked stem thorns. As with other thorny species the impalas and goats ate mainly single leaves of this species but the kudus ate the small lateral shoots of 2-3 inches in length regardless of the thorns.

The only common woody plant at Nylsvley with spiny leaves was S. pungens. The stiff evergreen leaves were angled towards the end of the shoot, each leaf terminating in a sharp spine. The impalas ate single leaves but the kudus, and occasionally the goats, ate whole shoots, biting through the stem with the molars then turning the shoot delicately around in the mouth until the leaf spines pointed away from the throat. When subjected to heavy browsing pressure this species forms dense clumps of very short shoots. The kudus were seen trying to fit these spiny masses of leaves into their mouths but usually gave up before obtaining any food. The impalas and goats could nibble leaves off the edge of these clumps but could not pull leaves from the centre of the clump.

b. Forbs

Few forbs bore structural defenses. The Asparagus species with their flexible stems, sharp hooks and small filamentous leaves were eaten by the impalas and goats which carefully nibbled the tiny leaves, but the kudus only ate these plants when the shoots were new and the thorns not yet hardened. Solanum species also have hooked stem thorns but the leaves are often large. The small spines on the midrib of the underside of each leaf of S. panduraeforme did not seem to effect the way the animals ate the plant but Solanum species were not favoured by the animals and are often reported to be toxic.

3. Experimental Removal of Thorns

a). Removal of Thorns From Trees in the Veld

Two months after the thorns were removed from branches of thorn trees in the veld, 80% of the thornless branches of A. nilotica and A. tortilis showed noticeably more browsing than was evident on the intact control branches. 60% of the thornless branches of

Table 6.8. Visual Estimate of the Increase (%) in Leaf Loss to Browsers on Branches with the Thorns or Spines Removed, as Compared to Paired Intact Branches

Tree Species	Acacia nilotica	Acacia tortilis (- hooks)	Acacia tortilis (+ hooks)	Acacia burkei	Dichrostachys cinerea
	80	80	0	80	80
	80	80	0	70	50
	80	40	0	50	40
	80	30	0	50	20
	50	20	-	20	-
	40	-	-	5	-
	40	-	-	0	-
	0	-	-	-	-
	0	-	-	-	-
Average	80	83	0	63	40
Difference from Zero (Values of Chi Squared)	4.234*	1.984	0.000	4.098*	1.680

* Significant at 95%

A. burkei showed increased browsing pressure in relation to the thorny branches but only four of the ten unarmed branches of D. cinerea were browsed more heavily than the spiny controls (Table 6.8.).

The increased browsing pressure on unarmed branches of A. nilotica and A. burkei was significantly different from zero, but for A. tortilis the sample size was too small as four of the branches were incompletely dethorned, having the hooked spines left on the branches and only the straight spines removed. The spines of D. cinerea were less effective in deterring large browsers than the sharp Acacia thorns, possibly because the leaves are larger than those of Acacias.

Interestingly of the four A. tortilis branches which had only the straight thorns, but not the small hooked thorns removed, none were browsed more than the intact branches. It seems that these small hooked thorns, which catch on the lips and tongue of the feeding animal, are a particularly effective defence strategy.

b). Branches Presented to Penned Goats

The intake rate achieved by the goats when feeding on A. tortilis increased significantly when the thorns were removed from the branches. This was due mainly to an increase in the feeding rate and to the greater quantity of food obtained per bite (Table 6.9.). A slight but non-significant increase was observed for the intake rate obtained from the other Acacia species once the thorns

Table 6.9 . The Effect of the Removal of Thorns and Spines from Branches of Armed Plants on the Feeding Behaviour of Goats.

Intake Rate (gms / min)

Species	Thorny		Thornless			
	Mean	SE	Mean	SE	n	t
Acacia nilotica	0.54 ±	0.06	0.87 ±	0.17	5	1.875
Acacia tortilis	0.31 ±	0.05	0.68 ±	0.09	6	3.700 **
Acacia burkei	2.61 ±	0.29	3.10 ±	0.33	6	1.270
Dichrostachys cinerea	2.53 ±	0.15	2.56 ±	0.22	5	0.113
Strychnos pungens	4.05 ±	1.05	9.48 ±	2.00	5	2.407 *

Feeding Rate (bites / min)

Species	Thorny		Thornless			
	Mean	SE	Mean	SE	n	t
Acacia nilotica	22.1 ±	4.79	28.9 ±	2.87	5	1.210
Acacia tortilis	19.6 ±	4.27	31.5 ±	2.25	6	2.469 *
Acacia burkei	24.5 ±	4.14	31.4 ±	2.07	6	1.491
Dichrostachys cinerea	32.6 ±	2.17	34.8 ±	3.86	5	0.498
Strychnos pungens	19.5 ±	3.81	27.1 ±	2.76	5	1.650

Bite Size (gms)

Species	Thorny		Thornless			
	Mean	SE	Mean	SE	n	t
Acacia nilotica	0.03 ±	0.00	0.05 ±	0.00	5	0.416
Acacia tortilis	0.01 ±	0.00	0.02 ±	0.01	6	0.100
Acacia burkei	0.11 ±	0.00	0.10 ±	0.01	6	0.149
Dichrostachys cinerea	0.10 ±	0.01	0.13 ±	0.01	5	0.302
Strychnos pungens	0.16 ±	0.02	0.33 ±	0.02	5	1.267

* Significant at 95%   ** Significant at 99%

had been cut off. Removal of the spines on D. cinerea branches had no effect upon the intake rate of the goats.

The spines of D. cinerea are less sharp than the Acacia thorns and are more widely spaced along the branches (Fig 6.10.), so were a less effective feeding deterrent to the goats. The leaf size of D. cinerea was also significantly larger than that of A. nilotica and A. tortilis. Both these species bear sharp straight thorns but A. tortilis also has small hooked thorns which catch the animals' lips. A. burkei has only large hooked thorns, although these caught the goats' lips and ears, the larger leaf size enabled the animals to obtain a similar intake to that from D. cinerea.

The leaves of S. pungens have sharp terminal spines. The shoots were eaten by the goats and kudus but were often shifted around in the mouth as though causing discomfort. When these leaf spines were removed the intake rate achieved by the goats doubled, due mainly to an increased bite size.

The deterrent effect of thorns and spines was further demonstrated by the goats, which soon learned to refuse the thorny branches presented to them and to wait until undefended branches were offered.

Table 6.10. The Distance (mm) Between the Thorns and Spines of Common Armed Woody Plant Species

Species	Distance Mean		SE	n
Dichrostachys cinerea	55.3	±	1.7	117
Acacia nilotica	37.1	±	1.1	93
Acacia tortilis (Straight)	30.6	±	1.4	61
Acacia tortilis (Hooked)	22.3	±	0.9	62

Differences Between The Spacing of Thorns

Species	t
Dichrostachys cinerea : Acacia nilotica	9.447***
Dichrostachys cinerea : Acacia tortilis (Straight)	11.279***
Acacia nilotica : Acacia tortilis (Straight)	3.658***
Acacia tortilis (Straight) : Acacia tortilis (Hooked)	4.929***

*** Significant at 99.9%

6.4. DISCUSSION

The effect of plant structure on the feeding behaviour of large herbivores is slightly different for each animal species due to their differing body size and feeding technique. The kudus were the largest of the three animal species considered. When feeding on non-thorny browse plants kudus ate mainly shoots. The impalas were the most delicate feeders, usually selecting single leaves. The goats were intermediate in their feeding behaviour, about a third of the bites taken by goats consisted of shoots and the remainder of leaves. The impalas had a more rapid rate of biting than the kudus and goats. Consequently the overall rate of food intake by the impalas and goats was similar at approximately 3g dry weight/min, while that of the kudus was 6g/min. The intake rate of the impalas, and to a lesser degree the goats, was naturally related to the leaf size of the plant. The weight of individual leaves was of less importance in determining the intake rate of the kudus as they eat mainly shoots.

The rate of feeding was negatively correlated to the bite size achieved when feeding on palatable woody plants. The bite size was particularly rapid when eating favoured food plants, most of which bear small leaves. Many of the favoured species are also armed. The presence of thorns and spines on the stems restricted the animals to eating single leaves or leaf clusters between the thorns. Although the rate of biting on these plants was high, this could not compensate for the low bite size achieved from the

Acacias and other thorny species bearing small leaves. When feeding on such plants the intake rate of the kudus was no greater than that of the impalas and goats.

In addition to limiting the bite size of the animal, the presence of thorns restricts the rate of feeding by large herbivores. Removal of the thorns from A. tortilis branches allowed the goats to increase their biting rate significantly. This effect was less marked for other armed species with larger leaves. A. tortilis combines a very small leaf size with both sharp straight thorns and small hooked thorns which catch on the animals lips and tongue so slowing down the rate of feeding. This effect was also noted by Dunham (1980) in his study of the feeding behaviour of a single tame impala in Sengwa, Zimbabwe. The spines of D. cinerea did not significantly reduce the intake rate of the impalas and goats because the leaves were fairly large, hence the bite size was greater than from the Acacia species. The intake rate of the kudus was low relative to unarmed species because the spines prevented the kudus from biting off whole shoots.

The spines on the leaves of S. pungens also reduced the rate of feeding by the animals, although the bite size was large since the kudus, and occassionally the goats, bite off shoots. These shoots must be carefully turned in the mouth until the sharp spines in the ends of the leaves face away from the throat before they can be swallowed, thus causing a delay in the rate of food intake.

The leaves of Acacias and D. cinerea were rich in nutrients as were the small leaves of G. flavescens. Yet due to the low rate of intake achieved from armed plants, the rate of ingestion nutrients from these species is often less than that achieved from relatively less nutrient rich plants with larger leaves. But many of the large leaved plants are also rich in fibre and digestion-reducing substances such as condensed tannins. All the animals showed a preference for the species offering leaves of high nutrient content and low condensed tannin content irrespective of the low rate of ingestion of these leaves. Browsers have a limited rumen capacity compared to that of grazers, hence must select their food for quality rather than quantity. Browsers are often termed as "concentrate selectors" (Hofmann & Stewart 1972).

Possibly unarmed plants with large leaves have a greater commitment to chemical defences than armed species. Certainly condensed tannins were prevalent in the larger leaved plants, but the total polyphenol content of the thorny A. nilotica was higher than that of all other plants. Since the structural deterrents can be of little effect against insects and microbes, the leaves of such species must also contain some chemical defences. The low acceptance of the animals for juvenile woody plants suggests they may be selecting against toxins. The juvenile growth form of many plants have a greater commitment to defence than the adult stages.

Despite the low intake rate achieved from armed plants such as Acacia and Ziziphus species, these plants are frequently the principal food of browsers (Knight 1965, Nge'the & Box 1976, Field & Ross 1976, Field 1978, Dunham 1980, Novellie 1983). In the Kruger National Park kudus were found to favour Acacia species in the wet season when food was abundant but to select the broad leaved species in the dry season (Novellie 1983). The animals at Nylsvley also increased their acceptance of large leaved plants in the dry season, but this was because the thorn trees are deciduous, and the few leaves remaining on the branches in the dry season and these disintegrated when touched.

Kudus seem to be more effectively deterred by the presence of thorns and spines than the smaller herbivores for which the lowering of the rate of food intake due to the presence of thorns is comparatively less than for kudus. Indeed the effectiveness of thorns was only noticeable in the intake rate of impalas and goats when the leaf size was very small. Acacia nigrescens was a staple food of kudus in the Kruger National Park, but they rarely ate the equally nutritious foliage of A. tortilis. The latter species has a much smaller leaf size and offers a very low rate of food intake. It was however well utilised by smaller browsers such as impala (Owen-Smith & Novellie 1983). Similarly at Nylsvley the Acacias, especially A. tortilis, were of lower acceptance to kudus than to the impalas and goats. Giraffe which are much larger animals than kudus eat A. tortilis, but employ a different feeding technique. The leaves are stripped off by the tongue instead of being bitten off (Pellew 1980). Milton (1980) noticed that stem thorns did not deter monkeys from feeding on certain tree species, such defences, no doubt, causing little trouble to the nimble fingers of these animals.

Some forbs also bear thorns, Asparagus species were often nibbled by the impalas and goats which could not possibly have obtained much food from the tiny filamentous leaves which grow in the angle between the stem and sharp thorns. The kudus were never seen to eat Asparagus plants except when the branches were young and the thorns still soft. The nutrient rich foliage of Solanum species was also rarely eaten, but several members of this genera is known to contain toxic alkaloids in addition to the structural defences.

Structural deterrents do not prevent feeding by large herbivores, but do reduce the rate of foliage loss to these animals by limiting the bite size achieved and possibly the rate of feeding. A combination of sharp thorns and a small leaf size was particularly effective in reducing the rate of foliage loss and severely reduced the food value of such plants, especially to the larger browsers such as kudus. Such structural defences however are not effective against insects and microbial pathogens, hence the leaves also require some chemical protection. Since thorns and spines are dead structures requiring little maintenance the occurrence of this form of double protection is feasible. Large leaved, unarmed plants would be expected to have a greater commitment to chemical defence than armed species which suffer reduced foliage loss to at least one category of enemy. The high palatability of armed species once the thorns are removed suggests that this is the case.

6.5. SUMMARY OF RESULTS

i. Impalas were delicate feeders eating mainly leaves. The size of the leaves was a determinant of the rate of food intake achieved by these animals. The goats ate both leaves and shoots, while the kudus ate mainly shoots.

ii. The rate of food intake achieved by the kudus was higher than that of the impalas and goats when feeding on unarmed plants, but when feeding on thorny plants there was little difference in the intake rate achieved by the three animal species. Hence the effects of thorns must be comparatively greater for the kudus than for the impalas and goats.

iii. The leaves of the thorny plants were rich in nutrients, but due to the low rate of food intake the rate of ingestion of nutrients from thorny plants was less than that achieved from less nutrient rich plants with larger leaves. Never the less the animals favoured the small leaved and thorny plants over many species of large leaved plants offering a higher rate of nutrient intake but also a much higher rate of intake of fibre and digestion-reducing compounds. i.e. the animals selected for plant quality rather than quantity.

iv. Thorns and spines did not deter feeding by large herbivores; indeed the leaves of many armed species are favoured by the animals. The possession of structural defences does however confer partial protection on the plant by limiting the bite size of the animals to single leaves, so minimising the rate of foliage loss to herbivores. The combination of sharp thorns and small leaves was particularly effective in minimising the bite size of large herbivores.

CHAPTER 7.

THE CHEMICAL BASIS OF SPECIES SELECTION BY BROWSING UNGULATES

7.1. INTRODUCTION

Much of the early work on factors influencing diet selection by large herbivores focused on domestic livestock which, with the exception of goats, are primarily grazers. Studies indicated that ruminants selected plants for their nutritional content, favouring those species rich in protein and low in fibre (Beaumont et.al. 1933, Irvines 1955, Cook 1959, Cowlishaw & Alder 1960, Thornton & Minson 1962, Arnold 1964, Burton et.al. 1964, Gangstad 1964, Heady 1964, Fontenot et.al. 1965).

Several studies have indicated that nutrient content is of importance in food selection of wild herbivores including lagomorphs (Miller 1968), primates (Struhsaker 1975, Casamir 1975, Chivers 1977, Hladick 1977, 1978, Nagy & Milton 1979) and ruminants (Klein 1970, Belovsky 1978, Leader-Willia· et.al. 1981, Pellew 1982, Vangilder et.al. 1982). Yet other studies found that diet selection could not be predicted for nutritional factors alone (Cowlishaw & Alder 1960, Bryant & Kuropat 1980, Sinclair et.al. 1984).

Browse plants, unlike grasses, often contain high levels of defensive chemicals. Freeland & Janzen (1974) proposed that plant species selection may be governed not by selection for nutrients, but by avoidance of plant secondary compounds deleterious to the fitness of th herbivore. Animals have frequently been shown to select against those plants richest in secondary compounds (Longhurst et.al. 1968, Radwan 1974, Levin 1976, Nagy et.al. 1977, Swain 1977, 1979, en 1978, Bryant 1980, 1981, Bryant & Kuropat 1980, Oates et.al. 1980, Pherson 1980).

Food selection however is most likely to be a complex process involving the selection of a balanced nutritional intake while at the same time avoiding the ingestion of deleterious levels of secondary compounds (Feeny 1970, Arnold & Hill 1972, Radwan & Crouch 1974, Slansky & Feeny 1977, Milton 1979, White & Trudell 1980, Kuropat & Bryant 1980, Glander 1981).

This selection process is constrained by the sensory capabilities of the herbivore. Arnold & Hill (1972) demonstrated that smell and taste were the most important senses in food selection, but sight and touch were also included.

The theory of "Nutritional wisdom" proposes that animals eat what is good for them since the sensory responses of the animal have been developed to give it adequate nutrition (Harborne 1972). Yet it is unlikely that the animal will have an integrated response to complex compounds such as protein (Arnold & Dudzinski 1978). Little is known about the sensory capabilities of herbivores to detect compounds in their food. Phosphorus deficient cattle made no attempt to rectify their deficiency when given a dicalcium phosphate lick (Cooper et.al. 1976). This suggests an inability to detect phosphorus. Yet sheep, elephants (Weir 1972) and reindeer (Staaland & Jacobsen 1980) will actively seek out sodium, presumably by its "salty" taste.

Animals generally prefer sweet flavours and are deterred by bitterness (Bate-Smith 1973) and astringency (Swain 1977). Many toxins are bitter, while astringency is a property of tannins. A natural aversion to bitterness could have been acquired by natural selection (Garcia & Hawkins 1974), but some nutritious and well utilised plants such as Bitterbush, _Purshia tridentata_, taste bitter to humans (Laycock 1978).

Few large herbivores are specialist feeders, but take a generalised diet including small quantities of a wide variety of plants. This generalised diet is thought to be an adaptation to the diversity of toxins in browse plants, by reducing the probability of the animal eating any one toxin in deleterious quantities (Freeland & Janzen 1974).

The detoxification of poisons is mainly due to the oxidisation of these substances by mixed function oxidase enzymes. These enzymes are common to most forms of life and are readily inducible (Brattsen 1979). It has been suggested that the microflora of ruminants have an important role in det ifying plant secondary chemicals and even that the rapid radiation of ruminants after the rise of the angiosperms in the paleocene is a result of predigestive detoxification by the rumenflora rendering potentially toxic compounds less harmful to the herbivore (Swain 1977, Foose & Lloyd 1974).

The possession of appropriate detoxification mechanisms may be a function of exposure. Thus grazers may be less well adapted to cope with the secondary chemicals present in browse. There are many records of browsers eating significant quantities of plants toxic to stock (Brynard & Pienaar 1960, Massay 1967, Goddard 1970).

In a similar manner it may be expected that alien herbivores may be more sensitive to the secondary chemicals in the plants than animals which have co-evolved with the vegetation.

7.2. METHODS

The acceptance of plant species by kudus, impalas and goats (see Chapter 5) was statistically compared with the concentrations of:-

i. Macronutrients - nitrogen, phosphorus, potassium, calcium, magnesium and sodium, and moisture contents,

ii. Fibre - neutral deterent fibre, neutral detergent fibre minus acid deterent fibre, acid detergent fibre and its components acid detergent lignin and acid detergent fibre minus acid detergent lignin.

iii. Digestion-reducing compounds - enzyme-inhibiting polyphenols, condensed tannins and ether-extractable materials.

Digestion-reducing compounds act in a dosage dependent manner. Toxic secondary compounds act in a qualitative way and are present in minute quantities, therefore only the presence or absence of alkaloids, cyanogenic glycosides, mono- and sesqui- terpenes and saponins was measured.

Analysis of soluble carbohydrates is both costly and time consuming. Concentrations within plant leaves vary greatly with photosynthetic rate (Mooney 1972) and it is unlikely that the animals can have an integrated response to "soluble carbohydrates" since sweetness is dependent upon molecular structure (Arnold & Hill 1972). Hence no analysis of soluble carbohydrates was done.

Neither were the plants analysed for trace elements. Facilities for analysis were not readily available and since there is doubt as to whether animals can detect macronutrients it is unlikely that concentrations of trace elements in the leaves can be detected by the herbivores.

The data were initially examined using techniques of regression. If a chemical factor influences food choice by herbivores, there should be a positive correlation between a measure of its concentration and a measure of food preference. Conversely if a factor causes avoidance of the plant species by herbivores then the correlation between its concentration and the preference of the animal should be negative.

Linear regressions were performed to test whether the correlations obtained were significantly different from chance. Regression analysis is very sensitive to extreme values. In the presence of extreme values a swarm of data points near the intercept tends to be treated as a single point (Peters 1983). Hence extreme values should be removed from the regression. The data often appeared to fall into groups rather than fitting a linear regression. Differences between these groups were compared by the randomisation test (Seigel 1956). This is a powerful test of location but can only be used when sample sizes are small and confidence can be placed in the numerical nature of the measurements obtained (Seigel 1956).

The chemical data were tested for skewness and kurtosis by the SAS statistical package (Means Procedure). Since the data proved to be of fairly normal distribution they were not transformed.

7.3. RESULTS

1. Nutrients

A. Woody Plants

a. Nitrogen

i. Kudus

There was no significant correlation between the acceptance of woody plants by the kudus, and the nitrogen content of the leaves, except in the early growing season when a significant positive correlation was evident (Fig 7.1.i.).

This correlation was spoilt in the late growing and early dry seasons by the high acceptance of V. rehmannii, which is of fairly low nitrogen content. However, on average the preferred plant species in these two seasons were of significantly higher nitrogen content than the less preferred species (Table 7.1.). In the late dry season there was an increase in the acceptance of most plant species retaining some leaves, including those species of low nitrogen content such as C. molle, T. sericea and the evergreens.

ii. Impalas

The acceptance of woody plants by impalas was not significantly